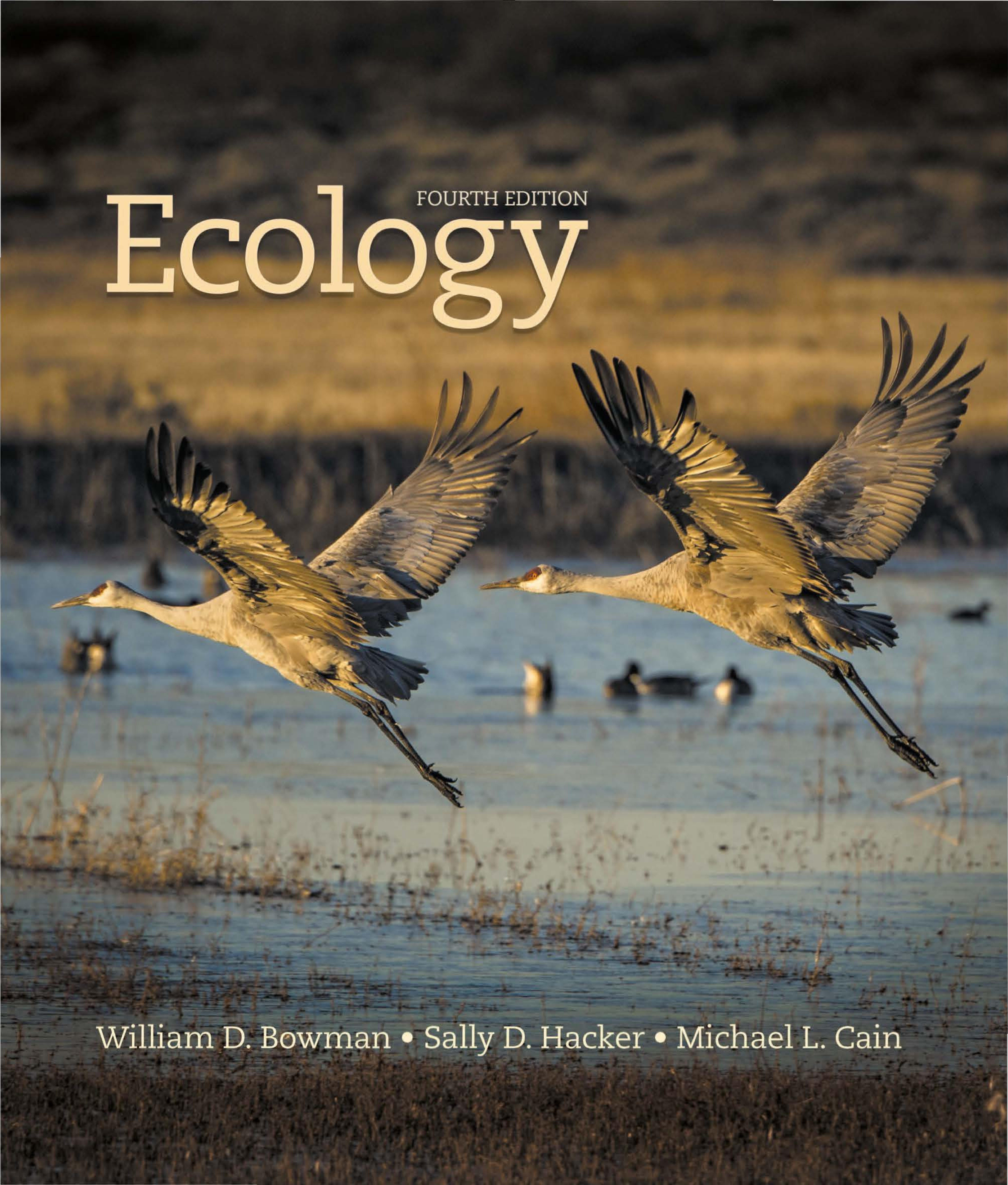
FOURTH EDITION

Ecology



William D. Bowman • Sally D. Hacker • Michael L. Cain

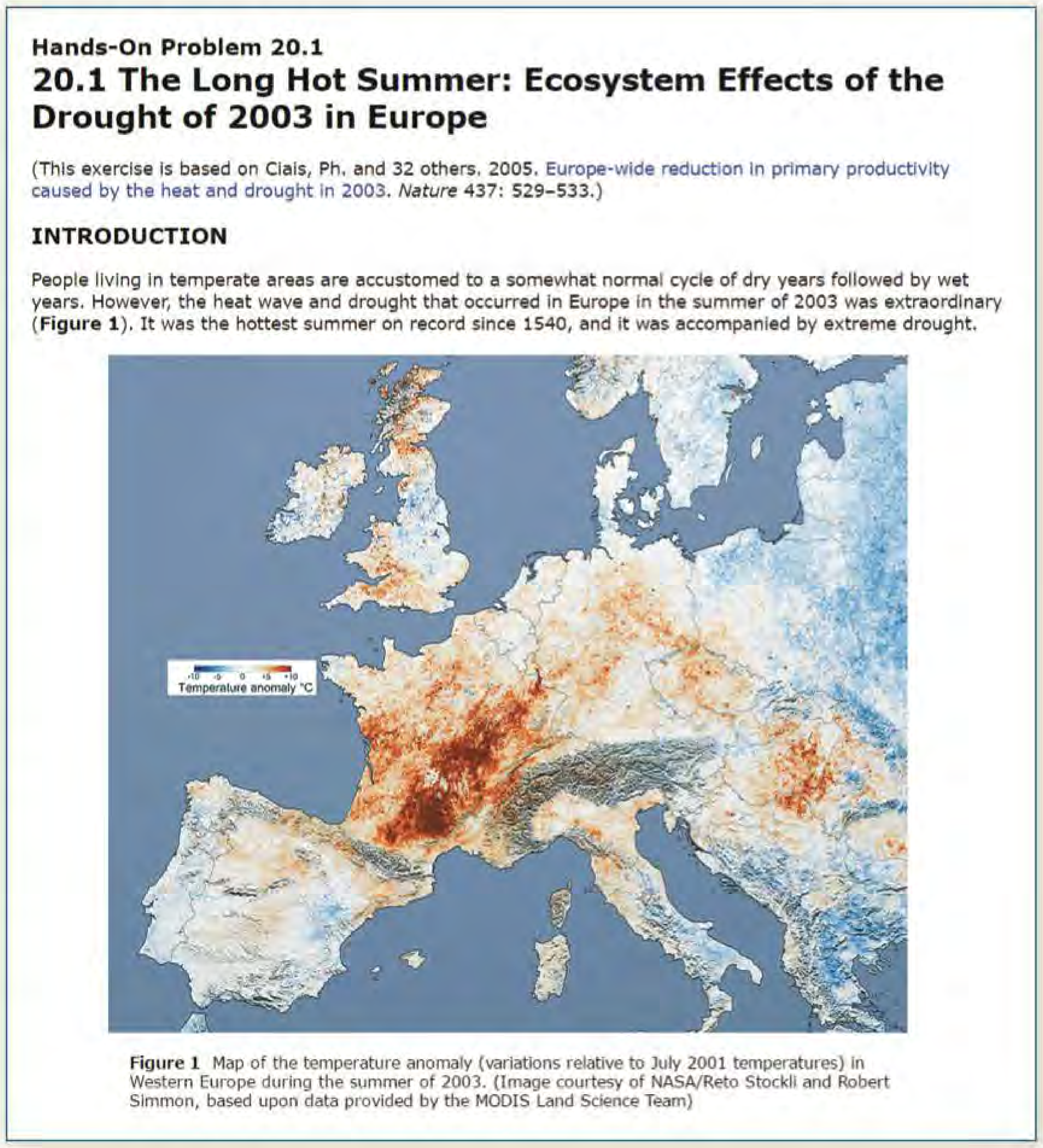
Ecology Fourth Edition

Companion Website

ecology4e.sinauer.com

The **Ecology** website is a companion to the textbook that can help you more effectively learn and review the material covered in your ecology course. The site is designed to help you master the concepts and terminology introduced in each chapter, and to apply that knowledge to real-world problems. The site includes the following resources:

- **Web Extensions** provide expanded and additional coverage of selected topics.
- **Hands-On Problems** (example shown at right) are inquiry-based exercises that challenge you to think as a scientist, analyze and interpret experimental data, and answer questions using simulations.
- **Climate Change Connections:** Expanded for the Fourth Edition, and now featured both in the textbook and online, Climate Change Connections help you better understand climate change by relating topics introduced in the textbook to other levels of the ecological hierarchy.
- **Web Stats Review** provides a brief review of statistical methods and techniques introduced in the textbook.
- **Online Quizzes:** These multiple-choice quizzes cover all of the main topics presented in each chapter. Your instructor may assign the quizzes, or they may be made available to you as self-study tools. (Instructor registration is required for student access to the quizzes.)



Hands-On Problem 20.1

20.1 The Long Hot Summer: Ecosystem Effects of the Drought of 2003 in Europe

(This exercise is based on Ciais, Ph. and 32 others. 2005. Europe-wide reduction in primary productivity caused by the heat and drought in 2003. *Nature* 437: 529–533.)

INTRODUCTION

People living in temperate areas are accustomed to a somewhat normal cycle of dry years followed by wet years. However, the heat wave and drought that occurred in Europe in the summer of 2003 was extraordinary (**Figure 1**). It was the hottest summer on record since 1540, and it was accompanied by extreme drought.

Figure 1 Map of the temperature anomaly (variations relative to July 2001 temperatures) in Western Europe during the summer of 2003. (Image courtesy of NASA/Reto Stockli and Robert Simmon, based upon data provided by the MODIS Land Science Team)

Also: **Outlines • Summaries • Suggested Readings • Flashcards • Glossary**

Access Instructions

To access the Companion Website, follow the instructions below to create an account and log in.

1. Go to **ecology4e.sinauer.com**
2. Click "Register."
3. Enter the registration code below and follow the on-screen instructions to create your account.
4. After registering, go to ecology4e.sinauer.com and log in using your newly-created login information.

Scratch below to reveal your unique registration code:

Important Note: The registration code above is valid for creating one account only.
If the code has been revealed, it may no longer be valid. New codes may be purchased at ecology4e.sinauer.com.

Hands-On Problems

The following Hands-On Problems are available on the Companion Website:

1.1 When a Mosquito Flaps Its Wings…: Connections in the Natural World: This exercise explores connections between periodic drought, mosquito populations, and the incidence of mosquito-transmitted diseases. A recent paper provides evidence that populations of mosquitos increase after severe droughts. You will consider the hypothesis that the mosquito-transmitted disease, West Nile Virus, increases after severe droughts, and discuss the implications of connections in natural systems.

2.1 Long, Long Ago in a Galaxy not Far Away: Seasonal Climate Variation and Axial Tilt on Habitable Planets: This exercise illustrates connections between the axial tilt of Earth and annual temperature variation. Seasonal patterns and the range of temperature variation across latitudes result from the degree of axial tilt. You will use a simulation model of Earth to vary axial tilt and explore seasonal variation in temperature across a range of latitudes.

3.1 Advance of the Tree Lines: Biome Boundaries and Climate Change: This exercise explores connections between elevation of tree lines and climate patterns. You will consider the results of a paper that discusses factors determining upper tree lines and which types of tree lines are likely to advance with changes in temperature. You will interpret plots of recent temperature changes in high elevation areas and discuss the probability of tree line advance there.

4.1 City Ants and Country Ants: Adaptation to Thermal Environments: This exercise explores thermal adaptation in ants that live in cities. You will interpret data from a recent paper about tolerance to high and low temperatures in ants that live in cities and ants that live in surrounding natural habitat. You will discuss the implications of the observed variation.

5.1 Some Like it Hot: Comparison of C_3 and C_4 Pathways: This exercise explores the conditions which favor C_3 or C_4 photosynthetic pathways. You will investigate the effects of temperature variation on growth of plants, and hypothesize about the conditions that favor alternative photosynthetic pathways. You will then test your predictions with a simulation model.

6.1 Drifting Down the River of Life: Natural Selection and Genetic Drift: This exercise demonstrates how natural selection and genetic drift can alter the frequencies of alleles in populations. With the use of a simulation model, you will investigate the effects of manipulating population sizes (and thus the strength of genetic drift) and the force of selection on genetic variation and persistence of variation in a population.

7.1 "You Can't Always Get What You Want": Life History Trade-Offs: This exercise explores the trade-off that organisms face between growth and reproduction. You will investigate the effects of manipulating the set point at which fish start allocating resources to reproduction rather than to growth under different levels of predation. You will use a simulation model to evaluate which strategies maximize fitness in differing environments.

8.1 Eating on a Budget: Balancing Costs and Benefits of Foraging: This exercise explores strategies predicted by optimal foraging under various conditions. Foraging decisions are based on relative costs and benefits. You will manipulate the foraging decision rules of a predator in a simulation model to explore how distance to and size of prey influence foraging strategies and resulting benefits.

9.1 Counting Beans: Effort and Accuracy of Population Estimates: This exercise illustrates the relationship between the effort required to obtain population size estimates and their accuracy. Species and population characteristics influence both the ease of obtaining population estimates and the accuracy of those estimates. With a simulation model, you will manipulate the amount of effort to explore the effects on estimate accuracy in two types of populations—fixed location and mobile species.

9.2 Taking Over the World: Correlates of Cosmopolitan Distributions: This exercise explores the species traits that promote cosmopolitan distributions of terrestrial tetrapods. You will review information from a recent paper on lineages with cosmopolitan distributions. You will consider traits that might contribute to broad distributions, and then discuss both the patterns observed and the implications of broad distributions.

10.1 Braving the Wild Frontier: Population Dynamics in the Arctic Ground Squirrel: This exercise explores the effects of density-dependent and density-independent factors on population growth or decline. You will compare data from populations of Arctic ground squirrels to determine the relative size of density-dependent and density-independent effects. You will compare and interpret effects on measures of reproductive success, survival, and population growth.

10.2 Millions of Babies, but Few Children: Life Tables for Barnacles: This exercise allows you to practice life table calculations on some classic data from barnacles. Barnacles produce millions of offspring, but few survive to adulthood. You will calculate l_x, S_x, and F_x, and then use these values to calculate net reproductive rate.

11.1 Bamboo, Rats, and Famine in the Far East: Population Overshoots and Carrying Capacity: This exercise explores how the periodic mass flowering of bamboo in southeast Asia leads to a chain of events that results in a population explosion of rats, devastation of rice crops, and widespread famine. You will use a simulation model of rat population growth to explore how the chain of events unfolds. You will manipulate carrying capacity and population growth rate to match documented changes, and then discuss the implications of population growth.

12.1 Wolves, Willows, and the Ecology of Fear: Cascading Effects of Predators: This exercise explores how the effects of predators can cascade through multiple trophic levels. You will review information from a recent review of predator-driven cascades in marine systems, and then use data from a study of wolves and elk to test for a trophic cascade.

12.2 The Ups and Downs of Predators: Predator–Prey Cycles: This exercise explores the dynamics of coupled predator/prey systems. You will use a simulation model to predict equilibrium conditions depending on characteristics of predators or prey. By manipulating the functional response and starting densities of predators and the carrying capacity and starting density of prey, you will explore joint predator/prey population dynamics and predict effects of invasive predators.

13.1 The Animal That Changed the World: Fleas, Rats, and the Black Death: This exercise explores the dynamics of host–pathogen systems using the Bubonic plagues of Europe as a model. You will evaluate potential scenarios for introduction of the plague to cities of a given size. You will then calculate the potential for the pathogen to spread given traits of the host and parasite, and discuss the ecological and evolutionary implications of parasitic interactions.

14.1 If You Can't Beat 'em, and You Can't Join 'em, Move Away: Competition-Induced Character Displacement: This exercise explores competition and possible ecological and evolutionary responses. You will review data from a recent paper on competition between two species of spadefoot toads and the development of two distinct tadpole morphologies—omnivore forms and carnivore forms—and discuss possible alternative explanations for the observed data.

15.1 A Double-Edged Sword: Costs and Benefits of Mutualisms: This exercise explores the dynamics of a mutualism between cacti and moths. You will review information from a recent paper that presents a model of this mutualism and discusses the natural history of the two species. Using a simulation model, you will explore the effects of starting population size and fruit abortion rate on the joint population dynamics of cacti and moths.

16.1 "Rich without Wealth": Richness and Diversity in Marine Sediments: This exercise explores the relationship between ecological diversity and species richness. You will use data from a recent paper on marine benthic invertebrates off the coast of Norway to compare patterns of diversity and richness among locations. You will then interpret patterns observed and discuss implications for community structure.

16.2 Diversity, the Spice of Life: Calculating Species Diversity: This exercise explores patterns of species diversity as affected by human impacts on the fish community in a Chilean river. You will calculate the Shannon index for several locations and compare patterns of diversity to historical data. You will interpret patterns in light of recent human impacts.

17.1 Starting Over in a Tropical Rainforest: Succession in Ants and Plants: This exercise explores patterns of succession in both plants and ants in a tropical rainforest in Mexico. You will review information from two papers that document succession on clear-cut plots of various ages. You will calculate the rate of successional change and the estimated time to reach climax conditions, and discuss implications for conservation and management.

18.1 Shining a Light on the Swiss Family Robinson: Diversity and Dynamics on Islands: This exercise explores the factors that determine the number of species that can occupy different islands according to the equilibrium theory of island biogeography. In a series of simulations, you will manipulate the size of an island and the distance from the island to the mainland to demonstrate how these factors interact to determine the equilibrium number of species on the island.

18.2 Why Size Matters: Island Size and Ecosystem Function: This exercise explores the relationship between forest fragment size and diversity and function of natural systems. You will review data from a recent study in which fragments or islands of once-continuous forest were experimentally created at different sizes. You will compare diversity and ecosystem function among fragments of different sizes and relate your findings to conservation and management.

19.1 What Goldilocks Can Teach Us about Coexistence: The Intermediate Disturbance Hypothesis: This exercise demonstrates how periodic disturbance allows more species to coexist in a community than otherwise would be able to as a result of competitive interactions. With a simulation model you will manipulate the frequency and intensity of disturbance to investigate the balance between competition and disturbance in determining how many species can coexist.

19.2 Does it Really Matter? Diversity and Productivity in Grasslands: This exercise explores the relationship between species diversity and ecosystem function in a grassland system. You will review a recent experimental study and interpret patterns of change observed with increased species diversity. You will interpret data and discuss the implications of loss of diversity in natural systems.

20.1 The Long Hot Summer: Ecosystem Effects of the Drought of 2003 in Europe: This exercise explores the effects of the 2003 drought in Europe on ecosystem productivity. You will review a recent paper and use data from the paper to calculate temperature and precipitation change from normal. You will explore relationships between temperature change and precipitation change and measures of ecosystem productivity.

20.2 The Cost of Staying Alive: Nitrogen and Energy in Subalpine Plants: This exercise explores the relationship between maintenance respiration costs and nitrogen availability. You will review information from a paper that documents the relationship between nitrogen content and respiration costs in subalpine plants. You will interpret and discuss the effect of nitrogen availability on productivity in ecosystems.

21.1 A Pound of Flesh: Trophic Efficiency in a Coral Reef: This exercise explores energy flow and efficiency of energy transfer in a coral reef system. You will review information from a recent paper that quantifies energy flow through multiple trophic levels in a community. Using data from the paper, you will calculate efficiencies at various levels in the system, and discuss the effect of trophic level on energy flow.

21.2 A Safe Place for My Children: Trophic Cascades and Neighborhood Effects: This exercise explores top-down effects of predators on community assembly of prey, with an emphasis on indirect effects. You will review information from a recent paper to interpret patterns of oviposition of aquatic insects based on the presence of predators and the proximity to predator-occupied habitats. You will then discuss the implications of indirect effects of predators on trophic cascades and energy flow.

22.1 Breaking it Down: Decomposition in Dry Environments: This exercise explores how plant litter decomposes in a dry climate. You will review information from a recent paper about relative effects of different factors responsible for litter decomposition in a semiarid ecosystem in Patagonia. You will interpret patterns in the data to compare the effect of light versus microorganisms in litter decomposition, and discuss implications for decomposition in other areas.

23.1 Not Dead Yet: Recovery of Endangered Species: This exercise explores the consequences of habitat restoration and augmentation of populations of endangered species with captive-reared individuals. You will use a transition matrix model to explore the effects of habitat restoration and population augmentation on population growth of an endangered fish, the June sucker.

24.1 You Can't Get There from Here: Movement in Heterogeneous Landscapes: This exercise explores how organisms move across different habitats in the landscape. You will use a simulation model to explore colonization patterns of different species in heterogeneous landscapes. You will then compare time to colonization to patterns of the connecting habitat corridor and movement traits of the species.

25.1 Too Much of a Good Thing: Anthropogenic Effects on the Global Nitrogen Cycle: This exercise explores global flows in reactive nitrogen from anthropogenic sources. You will review a recent paper on anthropogenic transformation of the global nitrogen cycle and then calculate gains and losses of nitrogen on a continental scale. You will then discuss the potential effects of changes in the nitrogen cycle on humans and the natural environment.

Ecology

Fourth Edition

FOURTH EDITION

Ecology

William D. Bowman • University of Colorado
Sally D. Hacker • Oregon State University
Michael L. Cain • New Mexico State University

Sinauer Associates, Inc. Publishers
Sunderland, Massachusetts, U.S.A.

On the Cover

Sandhill cranes (*Grus canadensis*) take off from their night refuge from predators en route to nearby fields to forage for the day. Bosque del Apache National Wildlife Refuge, New Mexico. Photograph © William D. Bowman.

Ecology, Fourth Edition

Address inquiries and orders to:
Sinauer Associates, Inc., P.O. Box 407, Sunderland, MA 01375-0407 U.S.A.

www.sinauer.com

FAX: 413-549-1118
E-mail: publish@sinauer.com

Library of Congress Cataloging-in-Publication Data

Names: Bowman, William D. | Hacker, Sally D. | Cain, Michael L. (Michael Lee), 1956-
Title: Ecology / William D. Bowman, University of Colorado, Sally D. Hacker, Oregon State University, Michael L. Cain, New Mexico State University.
Description: Fourth edition. | Sunderland, Massachusetts : Sinauer Associates, Inc., c2017. | Includes bibliographical references and index.
Identifiers: LCCN 2017002873 | ISBN 9781605356181
Subjects: LCSH: Ecology--Textbooks.
Classification: LCC QH541 .E31933 2017 | DDC 577--dc23
LC record available at https://lccn.loc.gov/2017002873

Printed in U.S.A.
5 4 3 2 1

For Jen, Gordon, and Miles and their unwavering support,
and to my students for pushing me as much as I pushed them.
WDB

For my family and my students, whose gift of time
has made all the difference.
SDH

For Debra and Hannah, with thanks and love.
MLC

About the Authors

William D. Bowman is a Professor at the University of Colorado at Boulder, affiliated with the Department of Ecology and Evolutionary Biology, Mountain Research Station, and the Institute of Arctic and Alpine Research. He earned his Ph.D. from Duke University. Dr. Bowman has taught courses in introductory ecology, plant ecology, plant–soil interactions, and ecosystems ecology, and for over two decades he has directed undergraduate summer field courses and research programs. His research focuses on the intersections of physiological ecology, community dynamics, and ecosystem function, particularly in the context of environmental change.

Sally D. Hacker is a Professor at Oregon State University, Corvallis, where she has been a faculty member since 2004. She has taught courses in introductory ecology, community ecology, and marine biology. She is particularly interested in promoting active and experiential learning for students interested in ecology and field experiences. Dr. Hacker's research explores the structure, function, and services of natural and managed ecosystems under varying contexts of species interactions and global change. She has conducted research with plants and animals in rocky intertidal, estuarine, and coastal dune ecosystems. Her work has most recently focused on the protective role of coastal ecosystems in mitigating the vulnerability from climate change. In addition to the textbooks, *Ecology* and *Life: The Science of Biology* (Sinauer), she is author or coauthor on numerous articles and book chapters exploring themes in community ecology and ecosystem functions and services.

William D. Bowman Sally D. Hacker Michael L. Cain

Michael L. Cain, having opted to focus full-time on writing, is affiliated with the Department of Biology at New Mexico State University. After receiving his Ph.D. in Ecology and Evolutionary Biology from Cornell University, he was a faculty member at New Mexico State University and the Rose-Hulman Institute of Technology. In addition to his work on this book, Dr. Cain is a coauthor of Campbell's *Biology* (Eleventh Edition) and *Biology in Focus* (Second Edition). He has instructed students across a wide range of subjects, including introductory biology, ecology, field ecology, evolution, botany, mathematical biology, and biostatistics. His research interests include: plant ecology; long-distance dispersal; ecological and evolutionary dynamics in hybrid zones; and search behavior in plants and animals.

Brief Contents

Preface

Ecology is at the heart of understanding our world—it serves as the glue that brings together information from a multitude of very different scientific disciplines, and it integrates this information in a way that informs us about how nature works. As our environment continues to change at an alarming rate it becomes increasingly critical that we improve our understanding of the repercussions of climate change, non-sustainable extraction of resources, the spread of invasive species, and pollution. Stewardship of resources that humanity requires—food, clean water, clean air, and many others—is best understood through the lens of ecological understanding.

Advances in ecology occur regularly, facilitated by technological and computational breakthroughs, as well as creative experimental research. This continued advancement, along with the diversity of subjects that form its basis, makes ecology a potentially daunting and complicated subject to learn and teach. Covering the breadth of ecology sufficiently in a textbook requires care so that students are not overwhelmed with the amount of material and instructors have adequate material to effectively engage students. With these challenges in mind, the overarching goal for the Fourth Edition of *Ecology* was to enhance the book as a learning tool for students and as a teaching tool for professors. To achieve these goals, the book's two core principles guided our every step.

Core Principles Guiding *Ecology*, Fourth Edition

This book is written for undergraduate students taking their first course in ecology. We set out to introduce our readers to the beauty and importance of ecology, and to do so without presenting them with too much material or boring them with unnecessary detail. While writing the Fourth Edition of *Ecology*, we kept our focus on two core principles: **"Teaching Comes First"** and **"Less Is More."**

Enabling effective teaching is our primary goal and motivation in *Ecology*. The structure and content of our chapters are designed primarily to make them good tools for teaching. For example, to introduce the material covered and capture student interest, each chapter begins with an engaging story (a "Case Study," as described more fully below) about an applied problem or interesting bit of natural history. Once students are drawn in by the Case Study, the "storyline" that it initiates is maintained throughout the rest of the chapter. We use a narrative writing style to link the sections of the chapter to one another, thus helping students keep the big picture in mind. In addition, the sections of the chapter are organized around a small number of Key Concepts (also described more thoroughly below) that were carefully selected to summarize current knowledge and provide students with a clear overview of the subject at hand. Similarly, when designing the art, pedagogy came first. Many students are visual learners, so we worked very hard to ensure that each figure "tells a story" that can be understood on its own.

As another way to help us achieve our primary goal of teaching students, we followed a "less is more" philosophy. We were guided by the principle that if we covered less material, but presented it clearly and well, students would learn more. Hence, our chapters are relatively short and they are built around a small number of Key Concepts (typically, three to five). We made these choices to prevent students from being overwhelmed by long, diffuse chapters, and to allow them to master the big ideas first. In addition, we put our "less is more" philosophy into action by asking each other whether the text served one of the following purposes:

- Does it help to explain an essential concept?
- Does it show how the process of ecological inquiry works?
- Does it motivate readers by focusing on a key ecological application or a fascinating piece of natural history?

This approach made for some tough choices, but it enabled us to focus on teaching students what is currently known about ecology without burdening them with excessive detail.

We also recognize that many instructors are choosing to "flip" their instructional style, with an emphasis on hands-on activities during classroom time and a greater reliance on student learning of core material outside of the classroom. *Ecology* serves this purpose well with its clear, easy-to-read, and well-organized presentation of material. In addition, there are several quantitative features—Analyzing Data exercises in the text and on the companion website, Hone Your Problem-Solving Skills and Hands-On Problem Solving exercises—that can serve as the basis for hands-on exercises.

New to *Ecology*, Fourth Edition

In striving to make *Ecology* the best teaching tool possible, we have updated, replaced, and edited sections of the text as appropriate. To accommodate the new features described below and keep the book to a manageable length, we have revised and cut some sections. The Fourth Edition includes:

Analyzing Data Exercises As part of their education students should become comfortable working with and analyzing data. Toward that end, we've added additional *Analyzing Data* exercises on the companion website. These online exercises give students extra practice with essential skills such as performing calculations, making graphs, designing experiments, and interpreting results.

Climate Change Connection Recognizing the increasing evidence for and effects of climate change on ecological systems, *Climate Change Connection* examples have been added into the main text of the book. These vignettes help students appreciate the many consequences of global climate change on the distributions and functions of organisms as well as the ecosystems they depend on. Nearly half of the chapters now include an in-text *Climate Change Connection*.

Hone Your Problem-Solving Skills The Fourth Edition features a new section added to the set of review questions at the end of each chapter. The *Hone Your Problem-Solving Skills* questions expose students to hypothetical situations or existing data sets, and allow them to work through data analysis and interpretation to better understand key ecological concepts and relate these concepts to real life situations.

Hallmark Features

In addition to the changes we just described, we've revised and strengthened the key pedagogical features of *Ecology*, introduced in previous editions:

Pedagogical Excellence Students taking their first course in ecology are exposed to a great deal of material, on a conceptual as well as individual-systems level. To help them manage this vast amount of information, each chapter of *Ecology* is organized around a small number of Key Concepts that provide up-to-date summaries of fundamental ecological principles.

Case Studies Each chapter opens with an interesting vignette—a *Case Study*. By presenting an engaging story or interesting application, the *Case Study* captures the reader's attention while introducing the topic of the chapter. Later, the reader is brought full circle with the corresponding "*Case Study Revisited*" section at chapter's end. Each *Case Study* relates to multiple levels of ecological hierarchy, thereby providing a nice lead-in to the *Connections in Nature* feature, described next.

Connections in Nature In most ecology textbooks, connections among levels of the ecological hierarchy are discussed briefly, perhaps only in the opening chapter. As a result, many opportunities are missed to highlight for students the fact that events in natural systems *really are* interconnected. To facilitate the ability of students to grasp how events in nature are interconnected, each chapter of *Ecology* closes with a section that discusses how the material covered in that chapter affects and is affected by interactions at other levels of the ecological hierarchy. Where appropriate, these interconnections are also emphasized in the main body of the text.

Online Climate Change Connection Climate change has broad ecological effects with important implications for conservation and ecosystem services. Half of the Fourth Edition chapters include an online climate change example. These *Climate Change Connection* vignettes link topics in the text to other levels of the ecological hierarchy, while enriching the student's understanding of ongoing climate change.

Ecological Inquiry Our understanding of ecology is constantly changing due to new observations and new results from ecological experiments and models. All chapters of the book emphasize the active, inquiry-based nature of what is known about ecology. This occurs throughout the narrative and is further highlighted by the *Analyzing Data* exercises discussed earlier, and by the *Figure Legend Questions* (described below). In addition, *Ecology* includes a similar online *Analyzing Data* exercise for every in-text *Analyzing Data* exercise, and hands-on interpretative and quantitative exercises, described next.

Hands-On Problem Solving Exercises This popular feature of the Companion Website asks students to manipulate data, explore mathematical aspects of ecology in more detail, interpret results from real experiments, and analyze simple model systems using simulations. Each chapter of the book includes one or more *Hands-On Problems*. These inquiry exercises can be used in two important ways: assigned as homework (all are available to students via the Companion Website), or used as in-class exercises (each is provided in a new instructor format that makes it easy to incorporate them into classroom sessions as active learning exercises or discussion topics).

Figure Legend Questions Each chapter includes 3–6 *Figure Legend Questions* that appear in maroon type at the end of the legend. These questions encourage students to grapple with the figure and make sure they understand its content. The questions range from those that test whether students understand the axes or other simple aspects of the figure to those that ask students to develop or evaluate hypotheses.

Ecological Applications In recent years, ecologists have increasingly focused their attention on applied issues. Similarly, many students taking introductory ecology are very interested in applied aspects of ecology. Thus, ecological applications (including conservation biology) receive great attention in this book. Discussions of applied topics are woven into each chapter, helping to capture and retain student interest.

Ecological Toolkits Nearly half of the chapters include an *Ecological Toolkit*, a box inset in the chapters that describes ecological "tools" such as experimental design, remote sensing, GIS, mark–recapture techniques, stable isotope analysis, DNA fingerprinting, and the calculation of species–area curves.

Links to Evolution Evolution is a central unifying theme of all biology, and its connections with ecology are very strong. Yet, ecology textbooks typically present evolution almost as a separate subject. As an alternative to the standard approach, the first chapter of *Ecology*'s Unit 2 (Chapter 6) is devoted to describing the joint effects of ecology and evolution. This chapter explores the ecology of evolution at both the population level and as documented in the sweeping history of life on Earth. Other topics in evolutionary ecology are explored in Chapter 7 (*Life History*) and in Chapter 8 (*Behavioral Ecology*). Concepts or applications that relate to evolution are also described in many other chapters.

Art Program Many of *Ecology*'s illustrations feature "balloon captions," which tell a story that can be understood at a glance, without relying on the accompanying text. The art program is available as part of the Instructor's Resource Library (see Media and Supplements).

Ecology Is a Work in Progress

This book, like the subject we write about, does not consist of a set of unchanging ideas and fixed bits of information. Instead, the book will develop and change over time as we respond to new discoveries and new ways of teaching. We would love to hear from you—what you like about the book, what you don't like, and any questions or suggestions you may have for how we can improve the book. You can reach us individually or as a group by sending an email message to ecology@sinauer.com, or by writing us at *Ecology*, Sinauer Associates, PO Box 407, Sunderland, MA 01375 USA.

Acknowledgments

We wish to express our appreciation to the people at Sinauer Associates, with whom we worked closely during the writing but especially during the book's production. Andy Sinauer supported the plan for the book from its inception. He enthusiastically participated in every phase along the way. Danna Lockwood and Kathaleen Emerson did a terrific job guiding the book through its many stages of production. Lou Doucette did a superb job of copyediting our manuscript. Elizabeth Morales provided the beautiful illustrations. David McIntyre and Martha Lorantos, our photo editors, always managed to find exquisite images that enhance the information in the figures. Joan Gemme facilitated several rounds of page design. We love her final version that you see here, as well as her elegant cover design. Dean Scudder masterminded the entire marketing effort and Marie Scavotto produced the attractive brochure. Mark Belk (Brigham Young University) and Amy Arnett (Unity College) expertly wrote and assembled the engaging online and instructor resources. These resources, along with the impressive array of supplements listed on pp. xiv and xv, were coordinated by Jason Dirks.

And finally, we'd like to thank some of the many people who helped us turn our ideas into a book in print. We are grateful to our colleagues who generously critiqued the plan for the book or read one or more chapters in manuscript; they are listed on the following pages. Among the hundreds of people we contacted while researching this book, we also wish to thank the following individuals for their special efforts in providing guidance and generously sharing their time and expertise: Jocelyn Aycrigg, Jenifer Hall-Bowman, John Jaenike, Michelle Koo, Karen Mabry, Debra VamVikites, and Tim Wright.

WILLIAM D. BOWMAN
william.bowman@colorado.edu

SALLY D. HACKER
hackers@oregonstate.edu

MICHAEL L. CAIN
mlcain@nmsu.edu

MARCH 2017

Reviewers

Reviewers for the Fourth Edition

Anita Baines, University of Wisconsin, La Crosse
Nate Bickford, University of Nebraska at Kearney
Brian Butterfield, Freed-Hardeman University
Kathleen Curran, Wesley College
John Fauth, University of Central Florida
Natalie Hyslop, University of North Georgia
Taegan McMahon, The University of Tampa
Luis Ruedas, Portland State University
Kathleen Schnaars Uvino, University of Jamestown

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Anita Baines, University of Wisconsin, La Crosse
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Andy Sih, University of California, Davis
Ted Stankowich, California State University, Long Beach
Diana Tomback, University of Colorado, Denver
Monica Turner, University of Wisconsin, Madison
Betsy Von Holle, University of Central Florida
Tobias Züst, Cornell University

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Stuart Allison, Knox College
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to accompany *Ecology*, Fourth Edition

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Ecology

Fourth Edition

1 The Web of Life

KEY CONCEPTS

CONCEPT 1.1 Events in the natural world are interconnected.

CONCEPT 1.2 Ecology is the scientific study of interactions between organisms and their environment.

CONCEPT 1.3 Ecologists evaluate competing hypotheses about natural systems with observations, experiments, and models.

Deformity and Decline in Amphibian Populations: A Case Study

In August of 1995, a group of elementary and middle school students from Henderson, Minnesota, made a gruesome discovery as they caught leopard frogs (*Lithobates pipiens*) for a summer science project: 11 of the 22 frogs they found were severely deformed. Some of the frogs had missing or extra limbs, others had legs that were too short or bent in odd directions, and still others had bony growths coming out of their backs (**Figure 1.1**). The students reported their findings to the Minnesota Pollution Control Agency, which investigated and found that 30%–40% of the frogs in the pond the students studied were deformed.

News of the students' discovery traveled fast, capturing public attention and spurring scientists to check for similar deformities in other parts of the country and in other amphibian species. It soon became apparent that the problem was widespread. In the United States, misshapen individuals were found in 46 states and in more than 60 species of frogs, salamanders, and toads. In some localities, more than 90% of the individuals were deformed. Deformed amphibians were also found in Europe, Asia, and Australia. Worldwide, it appeared that the frequency of amphibian deformities was on the rise.

Adding to the alarm caused by the gruesome deformities were observations, beginning in the late 1980s, of another disturbing trend: global amphibian populations seemed to be in decline. By 1993, over 500 populations of frogs and salamanders from around the world were reported to be decreasing in size or under threat of extinction. In some cases, entire species were in danger; across the globe, hundreds of species were extinct, missing, or critically endangered (**Figure 1.2**). Since 1980, at least 24 amphibian species have become extinct. An additional 113 species have not been seen since that time and are listed as "possibly extinct" (Vié 2009).

Species in other groups of organisms were also showing signs of decline, but scientists were especially worried about amphibians for three reasons. First, the decline appeared to have started recently across wide regions of the world. Second, some of the populations in decline were located in protected or pristine regions, seemingly far from the effects of human activities. Third, some scientists view amphibians as "biological indicators" of environmental conditions. They hold this view in part because amphibians have permeable skin (through which pollutants and other molecules can pass) and eggs that lack shells or other protective coverings. In addition, most amphibians spend part of their lives in water and part on land. As a result, they are exposed to a wide range of potential threats, including water and air pollution as well as changes in temperature and in the amount of ultraviolet (UV) light in their environment. Moreover, many amphibians remain close to their birthplace throughout their lives, so the decline of a local population is likely to indicate a deterioration of local environmental conditions.

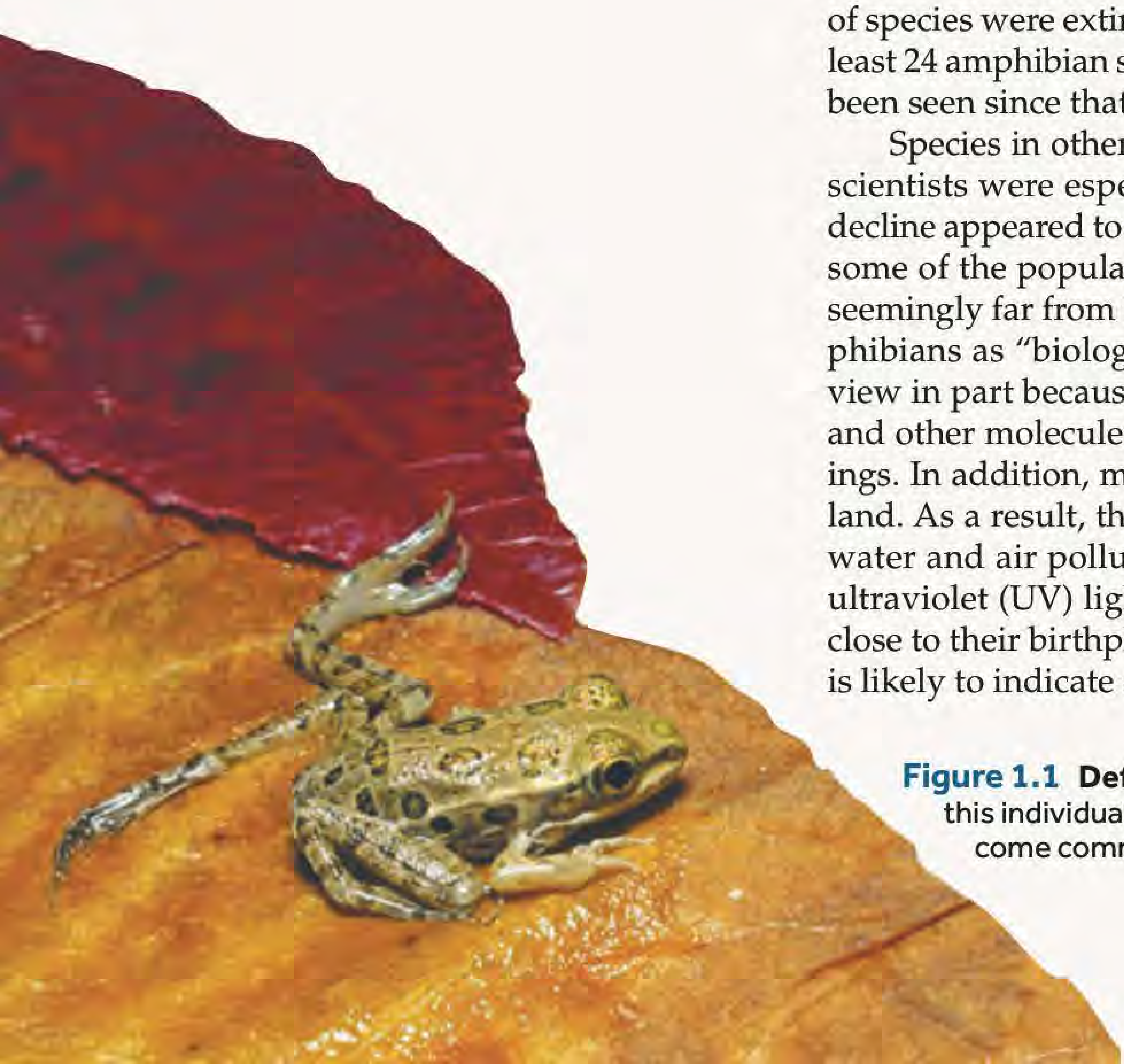


Figure 1.1 Deformed Leopard Frog With its misshapen and extra leg, this individual shows one of the types of limb deformities that have become common in leopard frogs and other amphibian species.

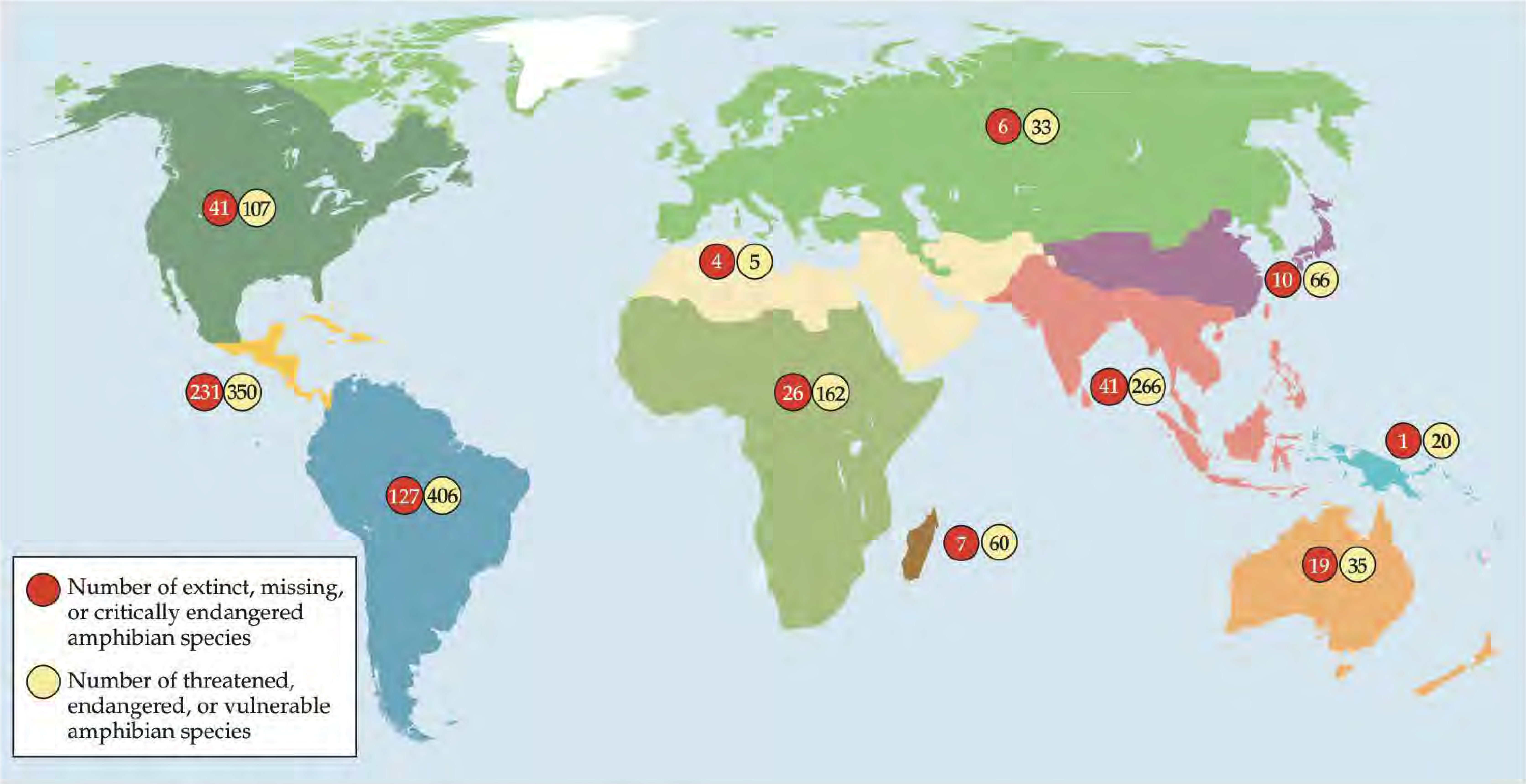


Figure 1.2 Amphibians in Decline In many regions of the world, amphibian species face increased risk of extinction. Each set of numbered balls is associated with one color-coded region on the map. (After Holt et al. 2013.)

Because amphibians worldwide were showing declining numbers and frequent deformities, scientists initially tried to find one or a few global causes that might explain these problems. However, as we'll see in this chapter, the story turned out to be more complicated than that: a single "smoking gun" has not emerged. What, then, has caused the global decline of amphibian populations?

Introduction

We humans have an enormous impact on our planet. Our activities have transformed nearly half of Earth's land surface and have altered the composition of the atmosphere, leading to global climate change. We have introduced many species to new regions, an action that can have severe negative effects on both native species and human economies. Even the oceans, seemingly so vast, show many signs of deterioration due to human activities, including declining fish stocks, the decline of once-spectacular coral reefs, and the formation of large "dead zones," regions where oxygen concentrations have dropped to levels low enough to kill many species.

Global changes like those we've just described can occur when humans take actions without giving much thought to how our actions might affect the environment. In such situations, we have repeatedly been surprised by the unintended and harmful side effects of our actions. Fortunately, we are beginning to realize that a better understanding of how the natural systems of our environment work can help us to anticipate the consequences of our actions and fix the problems we have already caused.

Our growing realization that we must understand how natural systems work brings us to the subject of this book. Natural systems are driven by the ways in which organisms interact with one another and with their physical environment. Thus, to understand how natural systems work, we must understand those interactions. *Ecology* is the scientific study of how organisms affect—and are affected by—other organisms and their environment.

In this chapter, we'll introduce the study of ecology and its relevance for humans. We'll begin by exploring a theme that runs throughout this book: connections in nature.

CONCEPT 1.1
Events in the natural world are interconnected.

Connections in Nature

From what you have read or observed about nature, can you think of examples that might illustrate the phrase "connections in nature"? In this book, we use that phrase to refer to the fact that events in the natural world can be linked or connected to one another. These connections occur as organisms interact with one another and with their physical environment. This does not necessarily mean that there are strong connections among all the organisms

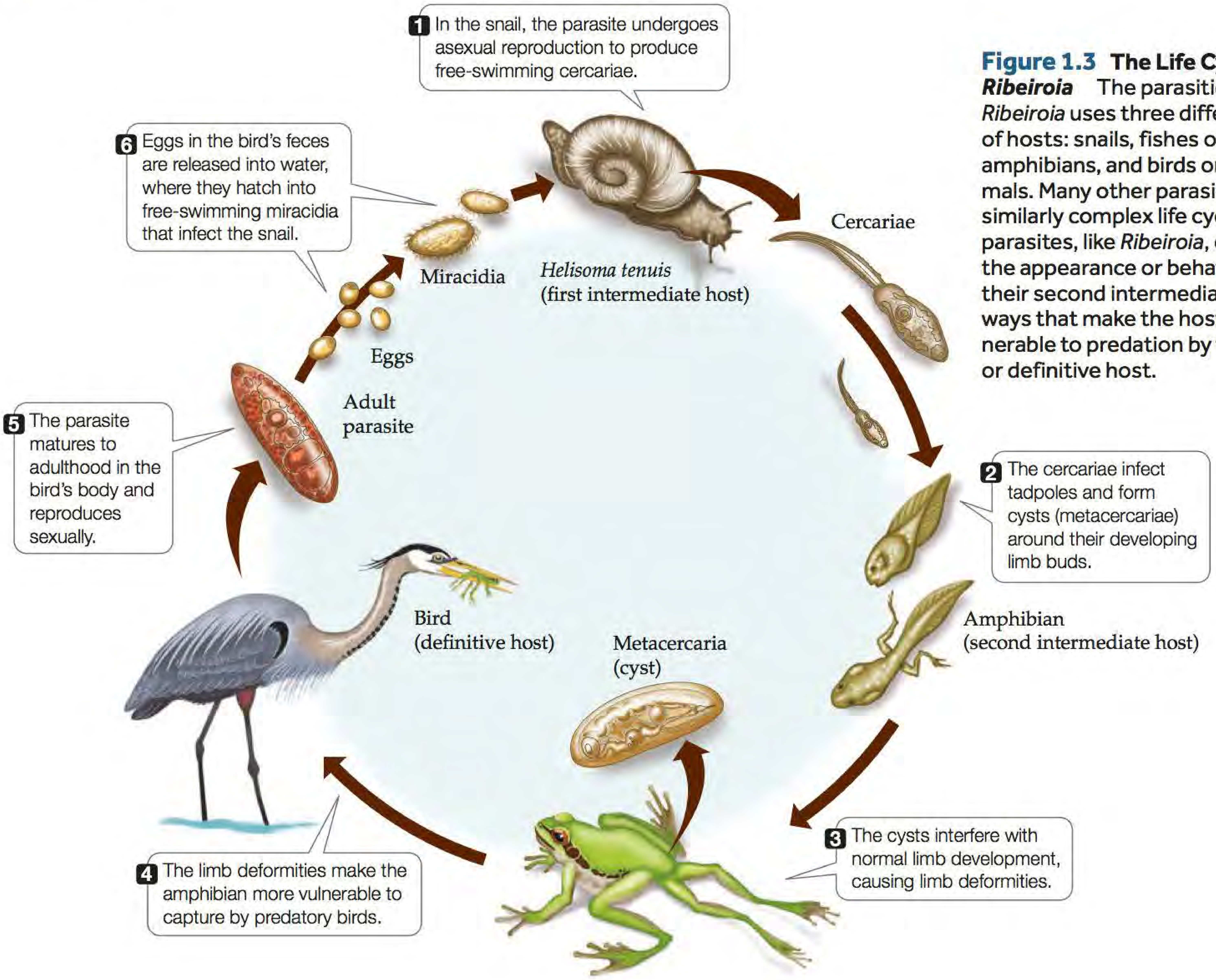


Figure 1.3 The Life Cycle of *Ribeiroia* The parasitic flatworm *Ribeiroia* uses three different kinds of hosts: snails, fishes or larval amphibians, and birds or mammals. Many other parasites have similarly complex life cycles. Some parasites, like *Ribeiroia*, can alter the appearance or behavior of their second intermediate host in ways that make the host more vulnerable to predation by their final or definitive host.

that live in a given area. Two species may live in the same area but have little influence on each other. But all organisms are connected to features of their environment. For example, they all require food, space, and other resources, and they all interact with other species and the physical environment as they pursue what they need to live. As a result, two species that do not interact directly with each other can be connected indirectly by shared features of their environment.

Connections in nature are revealed as ecologists ask questions about the natural world and examine what they've learned. To illustrate what this process can teach us about connections in nature, let's return to our discussion of amphibian deformities.

Early observations suggest that parasites cause amphibian deformities

Nine years before the Minnesota students made their startling discovery, Stephen Ruth was exploring ponds in Northern California when he found Pacific tree frogs (*Pseudacris regilla*) and long-toed salamanders (*Ambystoma macrodactylum*) with extra limbs, missing limbs, and other deformities. He asked Stanley Sessions, an expert in amphibian limb development, to examine his specimens. Sessions found that the deformed amphibians all contained a parasite, now known to be *Ribeiroia ondatrae*, a trematode flatworm. Sessions and Ruth hypothesized that the parasite caused the deformities. As an initial test of this hypothesis, they implanted small glass beads near the developing limb buds of tadpoles. These beads were meant to mimic the effects of *Ribeiroia*, which often produces cysts close to the areas where limbs form as a tadpole begins its metamorphosis into an adult frog. In a 1990 paper, Sessions and Ruth reported that the beads caused deformities similar to (but less severe than) those Ruth had found.

A laboratory experiment tests the role of parasites

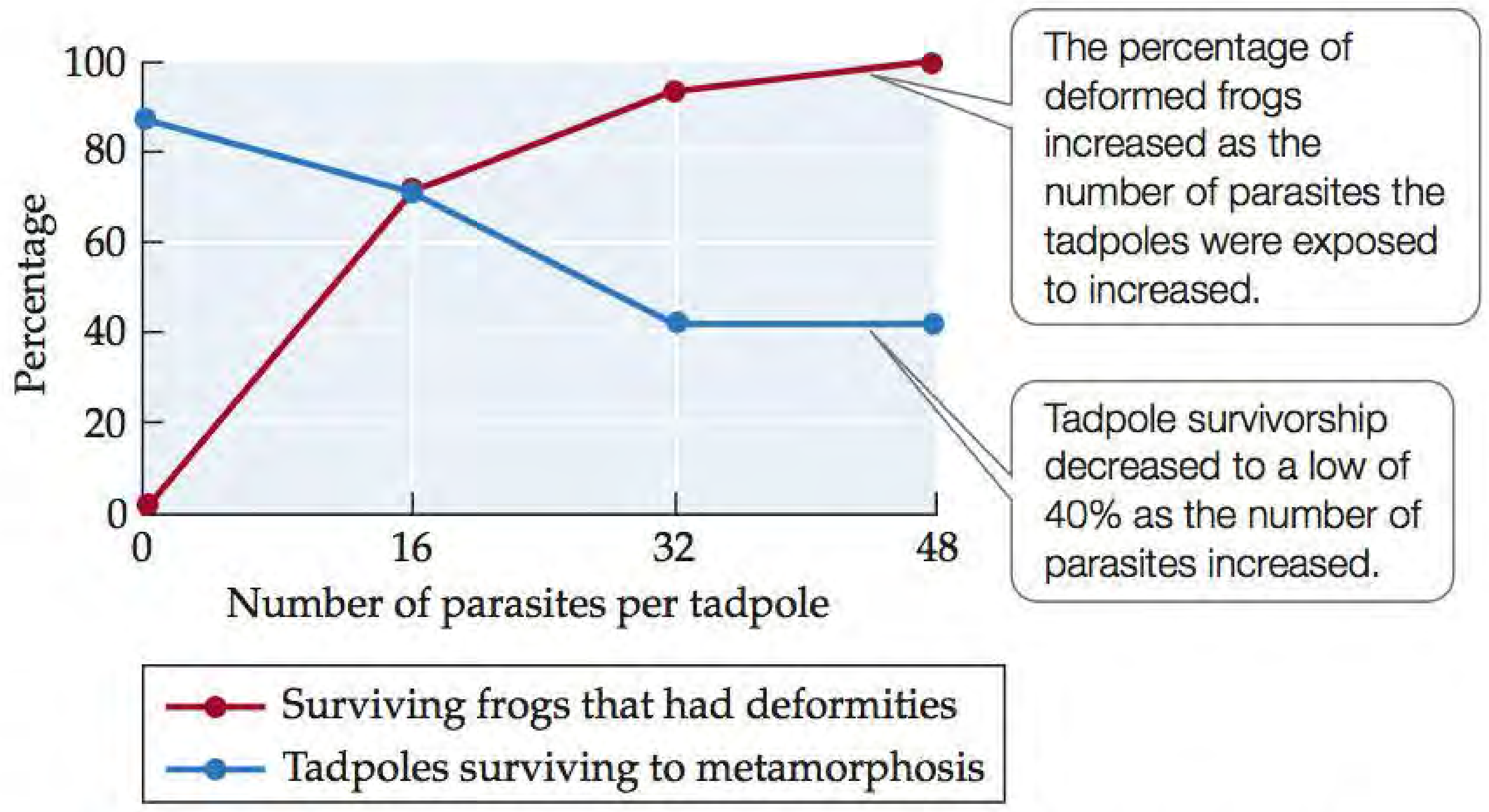
When Ruth first observed deformed amphibians in the mid-1980s, he assumed (quite reasonably) that they were an isolated, local phenomenon. By 1996, Pieter Johnson, then an undergraduate at Stanford University, had learned of the Minnesota students' findings and of the paper by Sessions and Ruth. Although Sessions and Ruth provided indirect evidence that *Ribeiroia* may have caused amphibian deformities, they did not infect *P. regilla* or *A. macrodactylum* with *Ribeiroia* and show that deformities resulted. Furthermore, the two amphibian species they used in their experiments (the African clawed frog, *Xenopus laevis*, and the axolotl salamander, *A. mexicanum*) were not known to have limb deformities in nature. Building on the work done by Sessions and Ruth (1990), Johnson and his colleagues set out to provide a more direct test of whether *Ribeiroia* parasites can cause limb deformities in amphibians.

They began by surveying 35 ponds in Santa Clara County, California. They found Pacific tree frogs in 13 ponds, 4 of which contained deformed frogs. Concentrating on 2 of these 4 ponds, they found that 15%–45% of the tadpoles undergoing metamorphosis had extra limbs or other deformities (Johnson et al. 1999). One source of concern was that the deformities might be caused by pollutants, such as pesticides, polychlorinated biphenyls (PCBs), or heavy metals. However, none of these substances were found in water from the 2 ponds.

Johnson and his colleagues then turned their attention to other factors that might cause the deformities. Aware that Sessions and Ruth had hypothesized that parasites could be the cause, Johnson et al. noted that of the 35 ponds they surveyed, the 4 ponds with deformed frogs were the only ponds that contained both tree frogs and the aquatic snail *Helisoma tenuis*. As shown in **Figure 1.3**, this snail is the first of two intermediate hosts required for the *Ribeiroia* parasite to complete its life cycle and produce offspring. The parasite also requires an amphibian or fish as a second intermediate host. In addition, dissections of abnormal frogs collected from the two ponds they studied in detail revealed *Ribeiroia* cysts in all the frogs with deformed limbs.

Like the findings of Sessions and Ruth, the observations described in the previous paragraph provided only indirect evidence that *Ribeiroia* caused deformities in Pacific tree frogs. Next, Johnson and his colleagues returned to the laboratory to perform a more rigorous test of that idea. They did this by using a standard scientific approach: they performed a **controlled experiment** in which an *experimental group* (that has the factor being tested) was compared with a *control group* (that lacks the factor being tested). Johnson et al. collected *P. regilla* eggs from a region not known to have frog deformities, brought the eggs into the laboratory, and placed the tadpoles that hatched from them in 1-liter containers (one tadpole per container). Each tadpole was then assigned at random to one of four *treatments*, in which 0 (the control group), 16, 32, or 48 *Ribeiroia* parasites were placed in its container; these numbers were selected to match parasite levels that had been observed in the field.

Johnson and his colleagues found that as the number of parasites increased, fewer of the tadpoles survived to metamorphosis, and more of the survivors had deformities (**Figure 1.4**). In the control group (with zero *Ribeiroia*), 88% of the tadpoles survived, and none had deformities (Johnson et al. 1999). The link had been made: *Ribeiroia* could cause frog deformities. Furthermore, since exposure to *Ribeiroia* killed up to 60% of the tadpoles, the results also suggested that the parasites could contribute to amphibian declines.



The percentage of deformed frogs increased as the number of parasites the tadpoles were exposed to increased.

Tadpole survivorship decreased to a low of 40% as the number of parasites increased.

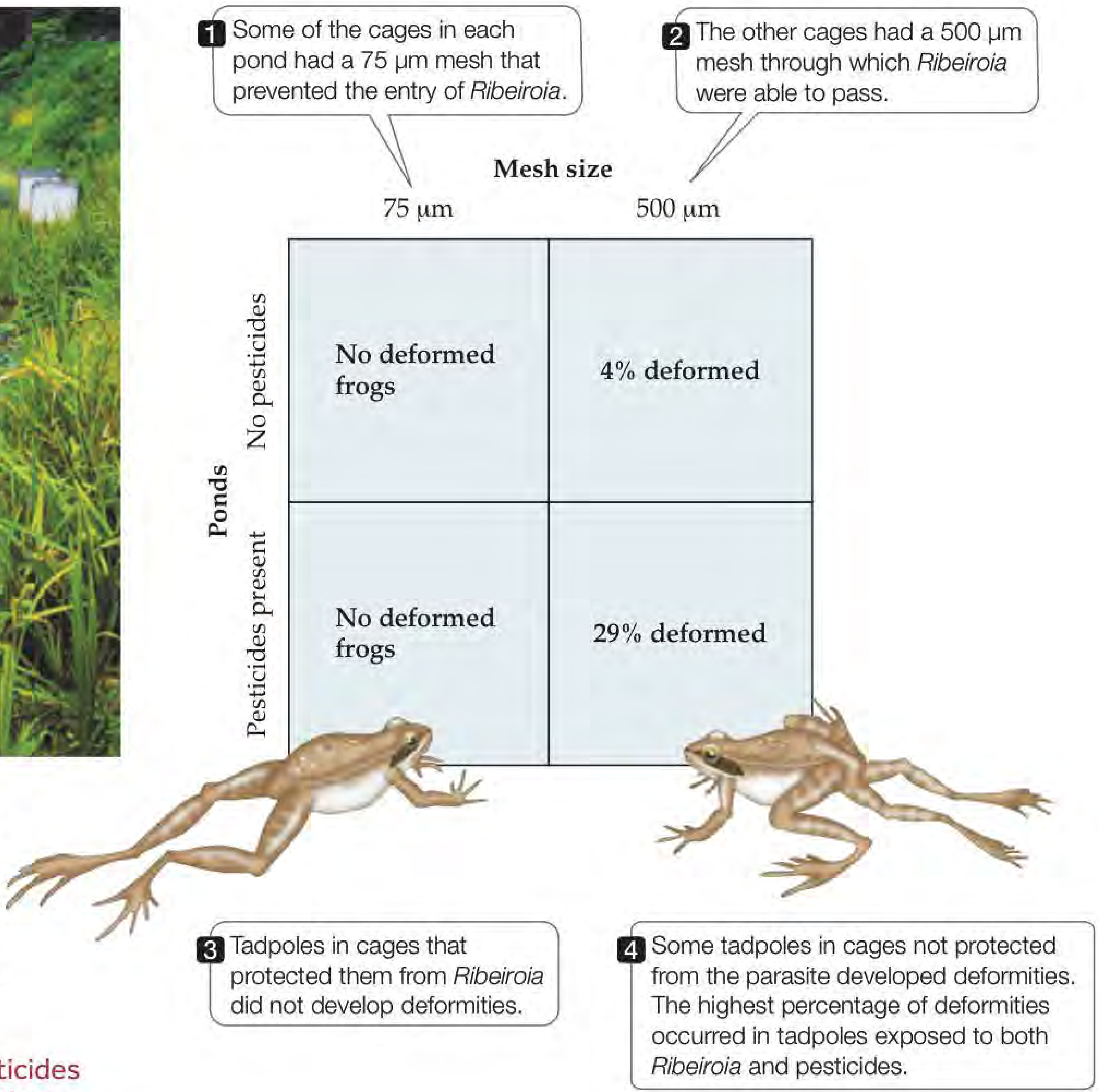
Figure 1.4 Parasites Can Cause Amphibian Deformities The graph shows the relationship between the numbers of *Ribeiroia* parasites that tadpoles were exposed to and their rates of survival and deformity. Initial numbers of tadpoles were 35 in the control group (0 parasites) and 45 in each of the other three treatments. (After Johnson et al. 1999.)

? Estimate the number of tadpoles in the control group that survived, as well as the number that had deformities.

A field experiment suggests that multiple factors influence frog deformities

A few years after Johnson and his colleagues published their research, other scientists showed that *Ribeiroia* parasites could cause limb deformities in other amphibian species, including western toads (*Anaxyrus boreas*), wood frogs (*Lithobates sylvaticus*), and leopard frogs (*L. pipiens*, the species in which the Minnesota students had discovered deformities). While *Ribeiroia* was clearly important, some researchers suspected that other factors might also play a role. Pesticides, for example, were known to contaminate some of the ponds in which deformed frogs were found. To examine the possible joint effects of parasites and pesticides, Joseph Kiesecker conducted a field experiment in six ponds, all of which contained *Ribeiroia*, but only some of which contained pesticides (Kiesecker 2002).

Three of the ponds in Kiesecker's study were close to farm fields, and water tests indicated that each of these ponds contained detectable levels of pesticides. The other three ponds were not as close to farm fields, and none of them showed detectable levels of pesticides. In each of the six ponds, Kiesecker placed wood frog tadpoles in cages made with a mesh through which water could flow but tadpoles could not escape. Six cages were placed in



1 Some of the cages in each pond had a 75 µm mesh that prevented the entry of *Ribeiroia*.

2 The other cages had a 500 µm mesh through which *Ribeiroia* were able to pass.

3 Tadpoles in cages that protected them from *Ribeiroia* did not develop deformities.

4 Some tadpoles in cages not protected from the parasite developed deformities. The highest percentage of deformities occurred in tadpoles exposed to both *Ribeiroia* and pesticides.

Figure 1.5 Do the Effects of *Ribeiroia* and Pesticides Interact in Nature? To test the effects of *Ribeiroia* and pesticides on frog deformities in the field, screened cages were placed in six ponds. Three of the six ponds contained detectable levels of pesticides; the other three did not. (After Kiesecker 2002.)

? Based on the results shown here, do pesticides acting alone cause frog deformities? Do the results indicate that pesticides affect frogs? If so, do they indicate how? Explain.

each pond; three of the cages had a mesh through which *Ribeiroia* parasites could pass, while the other three had a mesh too small for the parasites. Thus, in each pond, the tadpoles in three cages were exposed to the parasites, while the tadpoles in the other three cages were not.

The results showed that *Ribeiroia* caused limb deformities in the field (**Figure 1.5**). No deformities were found in frogs raised in cages whose small mesh size (75 µm) prevented the entry of *Ribeiroia*, regardless of which pond the cages were in. Deformities were found in some of the frogs raised in cages whose larger mesh size (500 µm) allowed the entry of *Ribeiroia*. In addition, dissections revealed that every frog with a deformity was infected by *Ribeiroia*. However, a greater percentage of frogs had deformities in the ponds that contained pesticides than in the ponds that did not (29% vs. 4%). Overall, the results of this experiment indicated that (1) exposure to *Ribeiroia* was necessary for deformities to occur, and (2) when frogs were exposed to *Ribeiroia*, deformities were more common in ponds with detectable levels of pesticides than in ponds without detectable levels of pesticides.

Based on these results, Kiesecker hypothesized that pesticides might decrease the ability of frogs to resist infection by parasites. To test whether pesticides had such an effect, Kiesecker (2002) brought wood frog tadpoles into the laboratory, where he reared some in an environment with pesticides and others in an environment without pesticides, then exposed all of them to *Ribeiroia*. The tadpoles exposed to pesticides had fewer white blood cells (indicating a suppressed immune system) and a higher rate of *Ribeiroia* cyst formation (**Figure 1.6**). Together, Kiesecker's laboratory and field results suggested that pesticide exposure can affect the frequency with which parasites cause deformities in amphibian populations. This conclusion has since been supported by other studies. Field surveys and laboratory experiments in Rohr et al. (2008), for example, indicated that exposure to pesticides can increase the number of trematode infections and decrease survival rates in several frog species. As in Kiesecker's study, one reason for the increased number of parasitic infections appeared to be that the frogs' immune response was suppressed by the pesticide.

Connections in nature can lead to unanticipated side effects

As we have seen, the immediate cause of amphibian deformities is often infection by *Ribeiroia* parasites. But we also noted in the Case Study that amphibian deformities

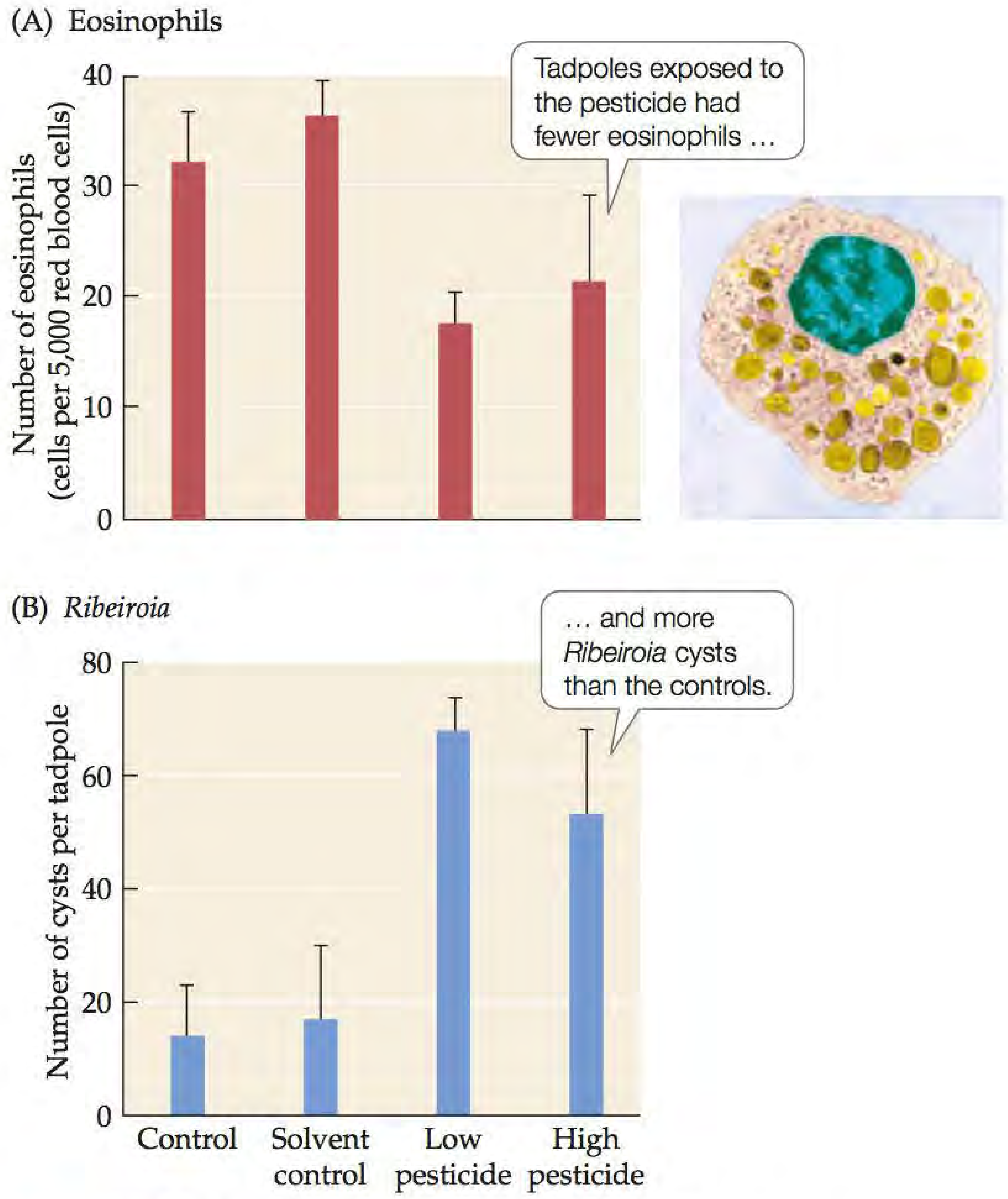


Figure 1.6 Pesticides May Weaken Tadpole Immune Systems In a laboratory experiment, wood frog (*Lithobates sylvaticus*) tadpoles were exposed to low or high concentrations of the pesticide esfenvalerate and then exposed to 50 *Ribeiroia* parasites per tadpole. The tadpoles were then examined for (A) numbers of eosinophils (a type of white blood cell used in the immune response) and (B) numbers of *Ribeiroia* cysts. Two types of controls were used: one in which only parasites were added to the tadpoles' containers ("control"), and another in which both parasites and the solvent used to dissolve the pesticide were added ("solvent control"). Error bars show one SE of the mean (see **Web Stats Review 1.1.2**). (After Kiesecker 2002.)

? What was the purpose of using two types of controls in this experiment?

are occurring more often now than in the past. Why has the frequency of amphibian deformities increased?

One possible answer is suggested by the results of Kiesecker (2002) and Rohr et al. (2008): pesticides may decrease the ability of amphibians to ward off parasite attack, and hence deformities are more likely in environments that contain pesticides. The first synthetic pesticides were developed in the late 1930s, and their use has risen dramatically since that time. Thus, it is likely that amphibian exposure to pesticides has increased considerably in recent years, which may help to explain the recent rise in the frequency of amphibian deformities.

Other environmental changes may also contribute to the observed increase in amphibian deformities. For example, the addition of nutrients to natural or artificial ponds (used to store water for cattle or crops) can lead to increases in parasite infections and amphibian deformities (Johnson et al. 2007). Nutrients can enter a pond when rain or snowmelt washes fertilizers from an agricultural field into it. Fertilizer inputs often stimulate increased growth of algae, and the snails that harbor *Ribeiroia* parasites eat algae (to refresh your memory of the parasite's life cycle, see Figure 1.3). Thus, as the algae increase, so do the snail hosts of *Ribeiroia*. An increase in snails tends to increase the number of *Ribeiroia* found in the pond.

Here, a chain of events that begins with increased fertilizer use by people ends with increased numbers of *Ribeiroia*, and hence increased numbers of deformed amphibians. As this example illustrates, events in the natural world are connected, one to another. As a result, when people alter one aspect of the environment, we can cause other changes that we do not intend or anticipate. When we increased our use of pesticides and fertilizers, we did not intend to increase the frequency of deformities in frogs. Nevertheless, we seem to have done just that.

The indirect and unanticipated effects of human actions include more than bizarre deformities in frogs. Indeed, some changes we are making to our local and global environment appear to have increased human health risks. The damming of rivers in Africa has created favorable habitat for snails that harbor trematode parasites that cause schistosomiasis, thereby increasing the spread of an infection that can weaken or kill people. Globally, the past few decades have seen an increase in the appearance and spread of new diseases, such as AIDS, Lyme disease, hantavirus pulmonary syndrome, Ebola hemorrhagic fever, and West Nile virus. Many public health experts think that the effects of human actions on the environment have contributed to the emergence of these and other new diseases (Weiss and McMichael 2004).

For example, West Nile virus, which is transmitted by mosquitoes and infects birds and humans, is thought to have been introduced into North America by people in 1999 (**Figure 1.7**). Furthermore, the incidence of West Nile virus in humans is influenced by factors such as human population size, the extent of land development, the abundance and identity of mosquito and bird species, and variations in temperature and rainfall (Reisen et al. 2006; Landesman et al. 2007; Allan et al. 2009). Each of these factors can be affected by human actions, either directly (e.g., by urban or agricultural development) or indirectly (e.g., as a result of climate change; see Concepts 25.2 and 25.3).

As we've seen, connections in nature can cause human actions to have unanticipated side effects. Moreover, if you live in a city, it can be easy to forget the extent to which everything you do depends on the natural world. Your house or apartment shelters you from the elements and keeps you warm in winter and cool in summer.

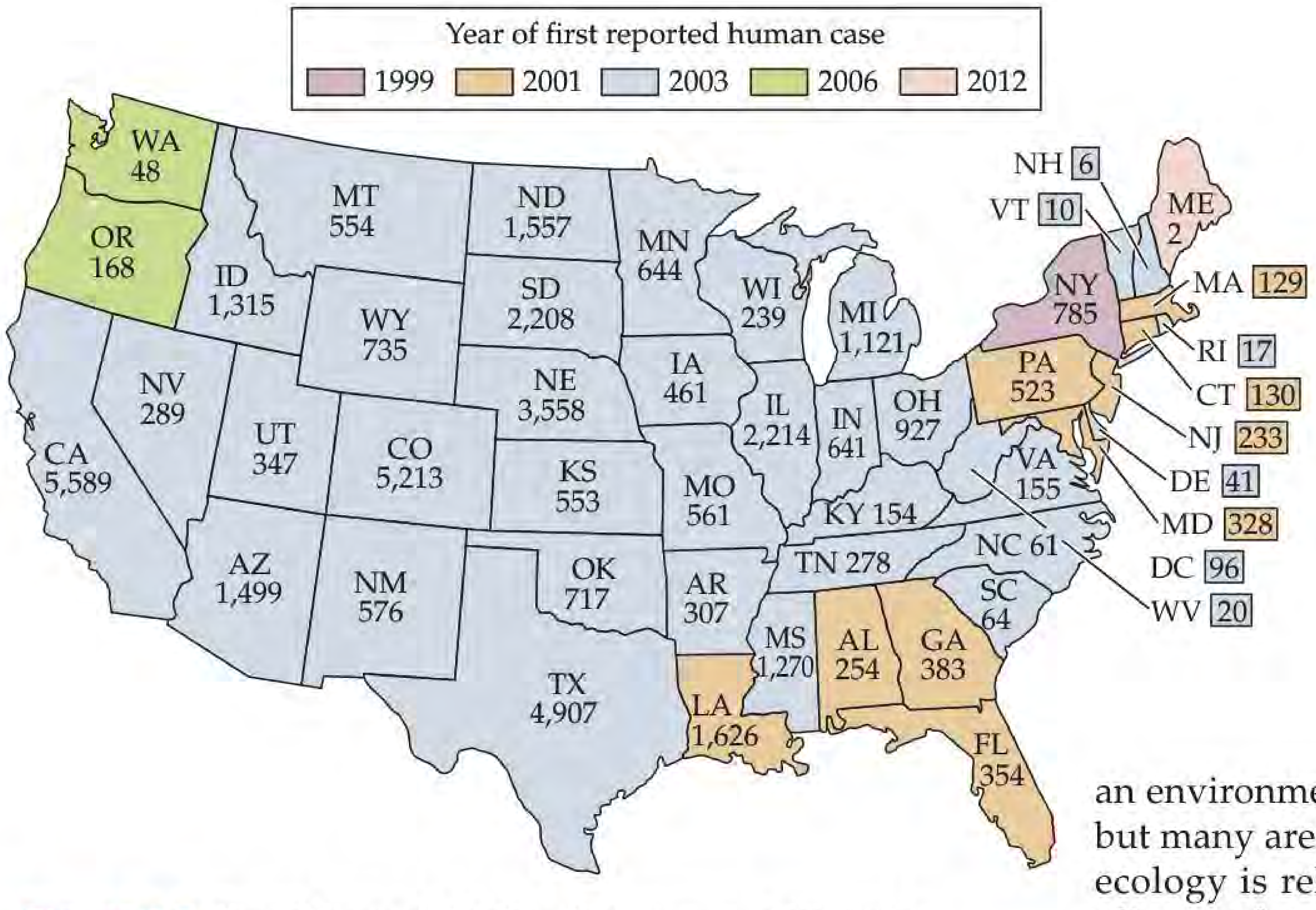


Figure 1.7 **Rapid Spread of a Deadly Disease** Within 13 years, West Nile virus had spread from its North American point of entry (New York City) to all of the lower 48 states. Birds are a primary host for West Nile virus, which may help to explain its rapid spread. Mosquitoes transmit the disease from birds and other animal hosts to people. Numbers show the cumulative number of human cases in each state by December 31, 2015. (Data from Centers for Disease Control and Prevention.)

? By what year had the disease spread to all but one of the lower 48 states? Identify the state(s) that were reached in that year, as well as the single state that had yet to be reached.

Similarly, you obtain food from a grocery store, clothes from a shop or department store, water from a faucet. Ultimately, however, each of these items—and everything else you use or own—comes from or depends on the natural environment. No matter how far from the natural world our day-to-day activities take us, people, like all other organisms on Earth, are part of an interconnected web of life. Let's turn now to the study of these connections, the scientific discipline of *ecology*.

CONCEPT 1.2
Ecology is the scientific study of interactions between organisms and their environment.

What Is Ecology?

In this book, **ecology** is defined as the scientific study of interactions between organisms and their environment. This definition is meant to include the interactions of organisms with one another because, as we have seen, organisms are an important part of one another's environment. Ecology can also be defined in a variety of other ways, such as the scientific study of interactions that determine the distribution (geographic location) and abundance of organisms. As will become clear as you read this book, these definitions of ecology can be related to one another, and each emphasizes different aspects of the discipline. A more important point for our purpose here is that the term "ecology," as used by ecologists, refers to a scientific endeavor.

We emphasize this point because "ecology" has other meanings in its public usage. People who are not scientists may assume that an "ecologist" is an environmental activist. Some ecologists are activists, but many are not. Furthermore, as a scientific discipline, ecology is related to—yet different from—other disciplines such as environmental science. Ecology is a branch of biology, while **environmental science** is an interdisciplinary field that incorporates concepts from the natural sciences (including ecology) and the social sciences (e.g., politics, economics, ethics). Compared with ecology, environmental science is focused more specifically on how people affect the environment and how we can address environmental problems. While an ecologist might examine pollution as one of several factors that influence the reproductive success of wetland plants, an environmental scientist might focus on how economic and political systems could be used to reduce pollution.

Public and professional ideas about ecology often differ

Surveys have shown that many members of the public think that there is a "balance of nature," in which natural systems are stable and tend to return to an original, preferred state after a disturbance, and that each species in nature has a distinct role to play in maintaining that balance. Such ideas about ecological systems can have moral or ethical implications for the people who hold them. For example, the view that each species has a distinct function can lead people to think that each species is important and irreplaceable, which in turn can cause people to feel that it is wrong to harm other species. As summarized by one interviewee in a survey on the meaning of ecology (Uddenberg et al. 1995, as quoted in Westoby 1997), "There is a certain balance in nature, and there is a place for all species. There is a reason for their existence and we are not free to exterminate them."

Public views on the balance of nature are not surprising, since these views were once held by many ecologists. However, ecologists now recognize (1) that natural systems do not necessarily return to their original state after a disturbance and (2) that seemingly random perturbations often play an important role in nature. In addition, as we will see in Unit 5, current evidence suggests that different communities can form in the same area under similar environmental conditions. Therefore, unless they provide careful qualifications, few ecologists today speak of a balance of nature.

While early views about a balance of nature have not stood the test of time, other ideas have. In particular, early ecologists and modern ecologists would agree that events in nature are interconnected (via the physical environment and via interactions among species). As a result, a change in one part of an ecological system can alter other parts of that system, including those that govern life-supporting processes such as the purification and replenishment of air, water, and soil.

Connections in nature form the basis for the first of eight ecological maxims that we will mention in this book, namely, "You can never do just one thing" (see **Table 1.1** for the full list). This maxim is meant to suggest that all actions have multiple effects because events in nature are interconnected. Overall, although the natural world may not be as predictable or as tightly woven as early ecologists may have thought, species are connected to one another. For some people, the fact that events in nature are interconnected provides an ethical imperative to protect natural systems. A person who feels an ethical obligation to protect human life, for example, may also feel an ethical obligation to protect the natural systems on which human life depends.

The scale of an ecological study affects what can be learned from it

Whether they study individual organisms or the diversity of life on Earth—or anything in between—ecologists always draw boundaries around what they observe. An ecologist interested in frog deformities might ignore the birds that migrate above the study site, while an ecologist studying bird migrations might ignore the details of what occurs in the ponds below. It is not possible or desirable to study everything at once.

When they seek to answer a particular question, ecologists must select the most appropriate dimension, or **scale**, in both time and space, for collecting observations. Every ecological study addresses events at some scales but ignores events at other scales. A study on the activities of soil microorganisms, for example, might be conducted at a small spatial scale (e.g., measurements might be collected at centimeter to meter scales). For a study addressing how atmospheric pollutants affect the global climate, on the other hand, the scale of observation would be large indeed and might include Earth's entire atmosphere. Ecological studies also differ greatly in the time scales they cover. Some studies, such as those that document how leaves respond to momentary increases in the availability of sunlight, concern events on short time scales (seconds to hours). Others, such as studies that use fossil data to show how the species found in a given area have changed over time, address events at much longer time scales (centuries to millennia or longer).

TABLE 1.1 Some Ecological Maxims

1. You can never do just one thing.
   Organisms interact with one another and with their physical environment. As a result, events in nature are connected, and what affects one organism or place can affect others as well.
2. Everything goes somewhere.
   There is no "away" into which waste materials disappear.
3. No population can increase in size forever.
   There are limits to the growth and resource use of every population, including our own.
4. There is no free lunch.
   An organism's energy and resources are finite, and increasing inputs into one function (such as reproduction) results in a trade-off in which there is a loss for other functions (such as growth).
5. Evolution matters.
   Organisms evolve or change over time—it is a mistake to view them as static. Evolution is an ongoing process because organisms continually face new challenges from changes in both the living and nonliving components of their environment.
6. Time matters.
   Ecosystems change over time. When we look at the world as we know it, it is easy to forget how past events may have affected our present, and how our present actions may affect the future.
7. Space matters.
   Abiotic and biotic environmental conditions can change dramatically from one place to another, sometimes across very short distances. This variation matters because organisms are simultaneously influenced by processes acting at multiple spatial scales, from local to regional to global.
8. Life would be impossible without species interactions.
   Species depend on one another for energy, nutrients, and habitat.

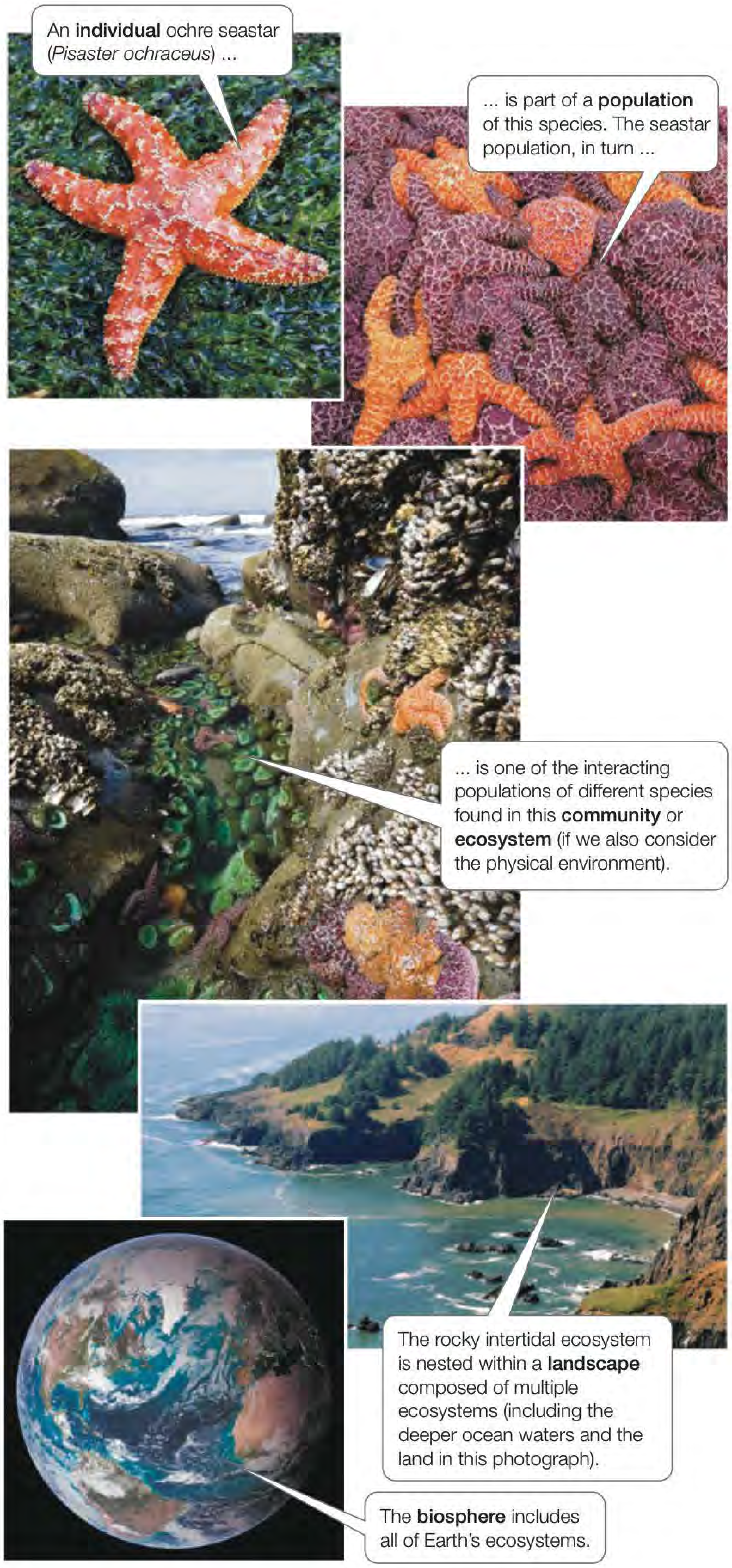
Ecology is broad in scope

Ecologists study interactions in nature across many levels of biological organization. Some ecologists are interested in how particular genes or proteins enable organisms to respond to environmental challenges. Other ecologists study how hormones influence social interactions, or how specialized tissues or organ systems allow animals to cope with extreme environments. However, even among ecologists whose research is focused on lower levels of biological organization (e.g., from molecules to organ systems), ecological studies usually emphasize one or more of the following levels: individuals, populations, communities, ecosystems, landscapes, or the entire biosphere (**Figure 1.8**).

A **population** is a group of individuals of a single species that live in a particular area and interact with one another. Many of the central questions in ecology concern how and why the locations and abundances of populations change over time. To answer such questions, it is often helpful to understand the roles played by other species. Thus, many ecologists study nature at the level of the **community**, which is an association of interacting populations of different species that live in the same area. Communities can cover large or small areas, and they can differ greatly in terms of the numbers and types of species found within them (**Figure 1.9**).

Ecological studies at the population and community levels often examine not only the effects of the **biotic**, or living, components of a natural system, but also those of the **abiotic**, or physical, environment. For example, a population or community ecologist might ask whether features of the abiotic environment, such as temperature, precipitation, or nutrients, influence the fertility of individuals or the relative abundances of the different species found in a community. Other ecologists are particularly interested in how ecosystems work. An **ecosystem** is a community of organisms plus the physical environment in which they live. An ecologist studying ecosystems might want to know the rate at which a chemical (such as nitrogen from fertilizers) enters a particular community, as well as how the species living there affect what happens to the chemical once it enters the community. For example, ecosystem ecologists studying amphibian deformities might document the rates at which nitrogen enters ponds that do and do not contain deformed amphibians, or they might determine how the presence or absence of algae affects what happens to nitrogen once it has entered the ponds.

Across larger spatial regions, ecologists study **landscapes**, which are areas that vary substantially from one place to another, typically including multiple ecosystems. Finally, global patterns of air and water circulation (see Concept 2.2) link the world's ecosystems into the **biosphere**, which consists of all living organisms on Earth plus the environments in which they live. The biosphere forms the highest level of biological organization. Over recent decades, as we will see in Unit 7, ecologists have acquired new tools that improve their ability to study the big picture: how the biosphere works. As just one example, ecologists can now use satellite data to answer questions such as, How do different ecosystems contribute to ongoing changes in the global concentration of carbon dioxide (CO_2) in the atmosphere?



An **individual** ochre seastar (*Pisaster ochraceus*) ...

... is part of a **population** of this species. The seastar population, in turn ...

... is one of the interacting populations of different species found in this **community** or **ecosystem** (if we also consider the physical environment).

The rocky intertidal ecosystem is nested within a **landscape** composed of multiple ecosystems (including the deeper ocean waters and the land in this photograph).

The **biosphere** includes all of Earth's ecosystems.

Figure 1.8 An Ecological Hierarchy As suggested by this series of photographs, life in the rocky intertidal ecosystem can be studied at a number of levels, from individuals to the biosphere. These levels are nested within one another, in the sense that each level is composed of groups of the entity found in the level below it.

Some key terms are helpful for studying connections in nature

Whether we are discussing individuals, populations, communities, or ecosystems, all chapters of this book incorporate the principle that events in the natural world are interconnected. For example, in Unit 3, we will see how an explosion in the population size of an introduced

Figure 1.9 A Few of Earth's Many Communities Moving counterclockwise, these photographs show (A) a savanna community in Serengeti National Park, Tanzania; (B) a rainforest canopy in the Amazon region of Ecuador; (C) an alpine meadow in bloom, Mount Rainier National Park, Washington, USA; and (D) a tropical coral reef in shallow waters of the Tubbataha Reef Natural Park, the Philippines. (B courtesy of Andrew Sinauer.)

species (the comb jelly *Mnemiopsis leidyi*) altered the entire Black Sea ecosystem. Because we stress connections in nature in every chapter, and hence may discuss ecosystems in a chapter about organisms, or vice versa, we describe here a handful of key terms that you will need to know as you begin your study of ecology. These terms are also summarized in **Table 1.2**.

A universal feature of living systems is that they change over time, or *evolve*. Depending on the questions or time scale of interest, **evolution** can be defined as (1) a change in the genetic characteristics of a population over time or as (2) *descent with modification*, the process by which organisms gradually accumulate differences from their ancestors. We will discuss evolution in the context

TABLE 1.2 Key Terms for Studying Connections in Nature

TERM	DEFINITION
Adaptation	A feature of an organism that improves its ability to survive or reproduce in its environment
Natural selection	An evolutionary process in which individuals that possess particular characteristics survive or reproduce at a higher rate than other individuals because of those characteristics
Producer	An organism that uses energy from an external source, such as the sun, to produce its own food without having to eat other organisms or their remains
Consumer	An organism that obtains its energy by eating other organisms or their remains
Net primary production (NPP)	The amount of energy (per unit of time) that producers fix by photosynthesis or other means, minus the amount they use in cellular respiration
Nutrient cycle	The cyclic movement of a nutrient between organisms and the physical environment

of ecology more fully in Chapter 6, but here we define two key evolutionary terms: "adaptation" and "natural selection."

An **adaptation** is a characteristic of an organism that improves its ability to survive or reproduce within its environment. Adaptations are of critical importance for understanding how organisms function and interact with one another. As we'll see in Concept 6.3, although several mechanisms can cause evolutionary change, only natural selection can produce adaptations consistently. In the process of **natural selection**, individuals with particular characteristics tend to survive and reproduce at a higher rate than other individuals *because of those characteristics*. If the characteristics being selected for are heritable, then the offspring of individuals favored by natural selection will tend to have the same characteristics that gave their parents an advantage. As a result, the frequency of those characteristics in a population may increase over time. If that occurs, the population will have evolved.

Consider what happens within the body of a person taking an antibiotic. Some of the bacteria that live inside that person may possess genes that provide resistance to the antibiotic. Because of those genes, those bacteria will survive and reproduce at a higher rate than will nonresistant bacteria (**Figure 1.10**). Because the trait on which natural selection acts (antibiotic resistance) is heritable, the offspring of the resistant bacteria will tend to be resistant. As a result, the proportion of resistant bacteria in the person's body will increase over time, and the bacterial population will have evolved.

The remaining four key terms that we'll introduce here concern ecosystem processes. One way to look at how ecosystems work is to consider the movement of energy and materials through a community. Energy enters the community when an organism such as a plant or bacterium captures energy from an external source, such as the sun, and uses that energy to produce food. An organism that can produce its own food from an external energy source without having to eat other organisms or their remains is called a **producer** (such organisms are also called *primary producers* or *autotrophs*). An organism that obtains its energy by eating other organisms or their remains is called a **consumer**. Per unit of time, the amount of energy that producers capture by photosynthesis or other means, minus the amount they lose as metabolic heat in cellular respiration, is called **net primary production** (**NPP**). Changes in NPP can have large effects on ecosystem function, and NPP varies greatly from one ecosystem to another.

Each unit of energy captured by producers is eventually lost from the ecosystem as metabolic heat (**Figure 1.11**). As a result, energy moves through ecosystems in a single direction only—it cannot be recycled. Nutrients, however, are

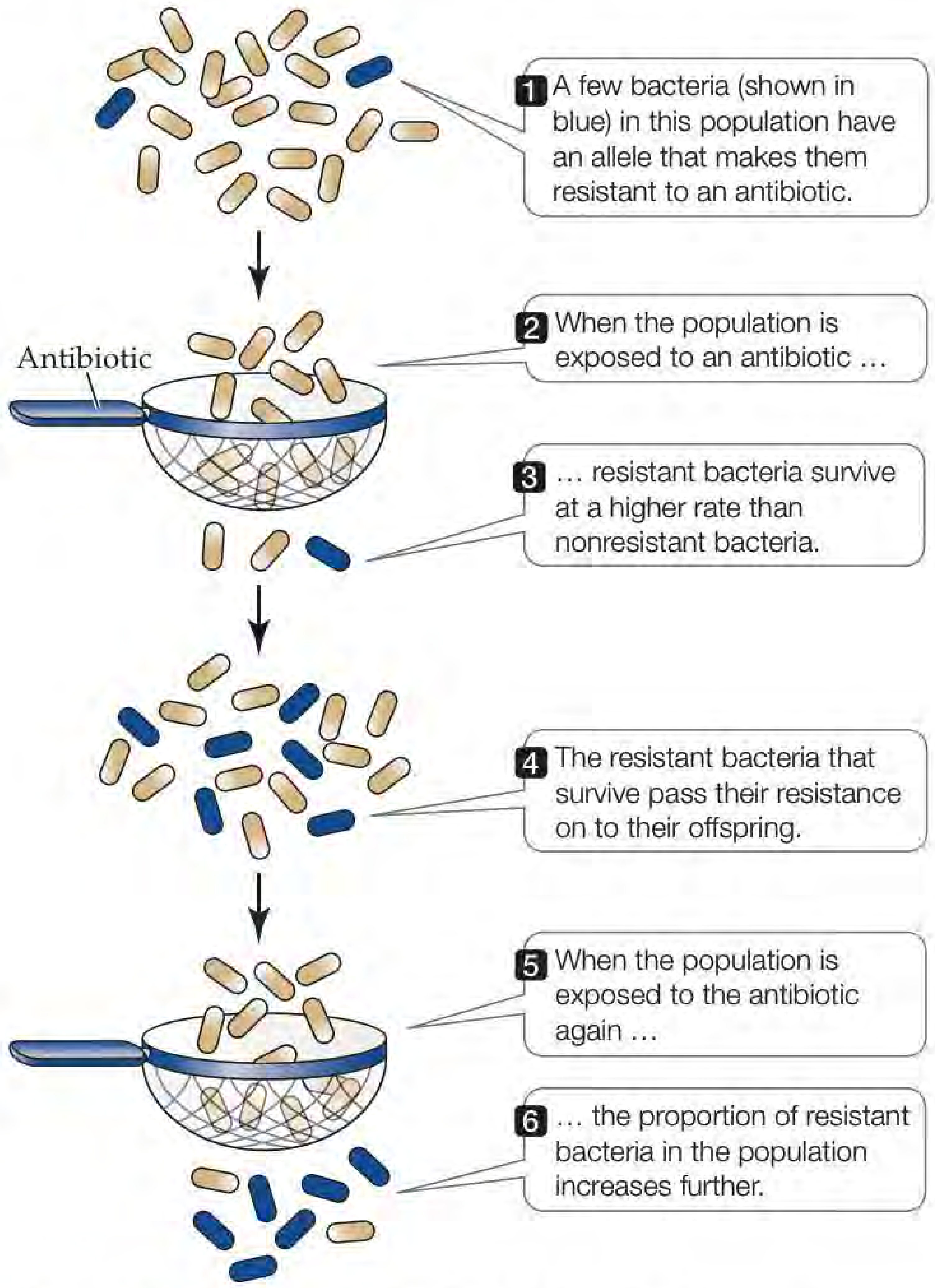


Figure 1.10 Natural Selection in Action As shown in this diagram, in which a sieve represents the selective effects of an antibiotic, natural selection can cause the frequency of antibiotic resistance in bacteria to increase over time.

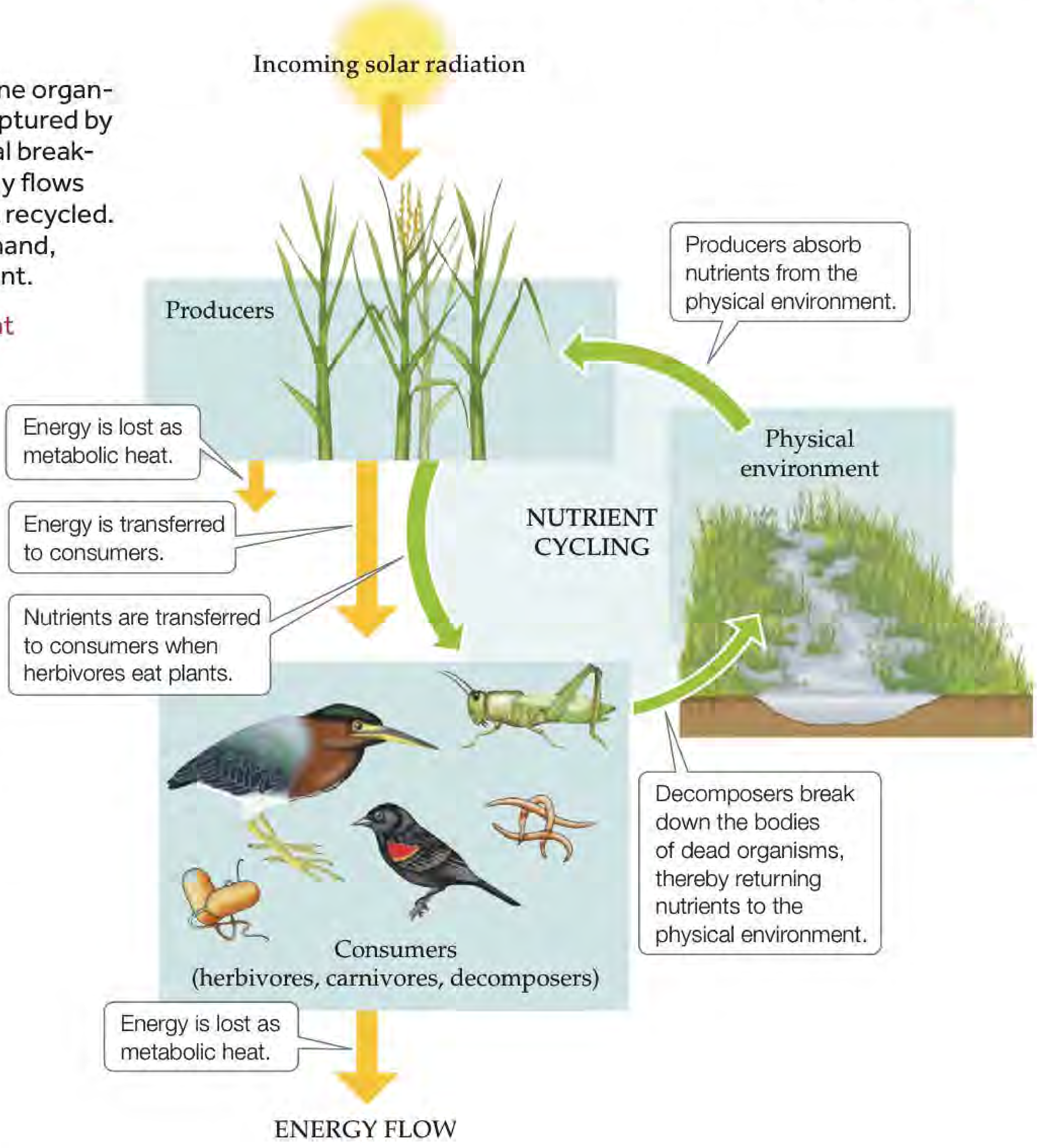


Figure 1.11 How Ecosystems Work Each time one organism eats another, a portion of the energy originally captured by a producer is lost as heat given off during the chemical breakdown of food by cellular respiration. As a result, energy flows through the ecosystem in a single direction and is not recycled. Nutrients such as carbon and nitrogen, on the other hand, cycle between organisms and the physical environment.

? Describe the three main steps by which a nutrient cycles through an ecosystem.

recycled from the physical environment to organisms and back again. The cyclic movement of a nutrient such as nitrogen or phosphorus between organisms and the physical environment is referred to as a **nutrient cycle**. Life as we know it would cease if nutrients were not recycled, because the molecules organisms need for their growth and reproduction would be much less readily available.

Whether they are concerned with adaptations or NPP, populations or ecosystems, the scientists who study ecological systems have not produced a fixed body of knowledge, engraved in stone. Instead, what we know about ecology changes constantly as ideas are tested and, if necessary, revised or discarded as new information emerges. As we will see in the next section, ecology, like all branches of science, is about answering questions and seeking to understand the underlying causes of natural phenomena.

CONCEPT 1.3

Ecologists evaluate competing hypotheses about natural systems with observations, experiments, and models.

Answering Ecological Questions

The studies of amphibian deformities that we discussed earlier in this chapter illustrate several ways in which ecologists seek to answer questions about the natural world. The study by Johnson and his colleagues (1999), for example, had two key components: observational studies in the field and a controlled experiment in the laboratory. In the observational part of their work, the researchers surveyed ponds, noted the species present, and observed that tree frog deformities were found only in ponds that contained both tree frogs and a snail that harbored the *Ribeiroia* parasite. These observations suggested that *Ribeiroia* might cause deformities, so Johnson and his colleagues performed a laboratory experiment to test whether that was the case (it was).

Kiesecker (2002) extended these results in two experiments, one performed in the field, the other in the laboratory. To examine the effects of pesticides on frog deformities, Kiesecker compared results from three ponds with pesticides with results from three ponds without detectable levels of pesticides. While this approach had the advantage of allowing the effects of *Ribeiroia* to be examined under different field conditions (in ponds with and without pesticides), Kiesecker could not control the conditions as precisely as he did in his laboratory experiment. The constraints of working in the field meant, for example, that he could not start out with six identical ponds, then add pesticides to three of them but not to the other three—an experiment that would test more directly whether pesticides were responsible for the results he obtained. As this example suggests, no single approach works best in all situations, so ecologists use a variety of methods when seeking to answer ecological questions.

Ecologists use experiments, observations, and models to answer ecological questions

In an ecological experiment, an investigator alters one or more features of the environment and observes the effect of that change, a procedure that allows scientists to test whether one factor has a cause-and-effect relationship

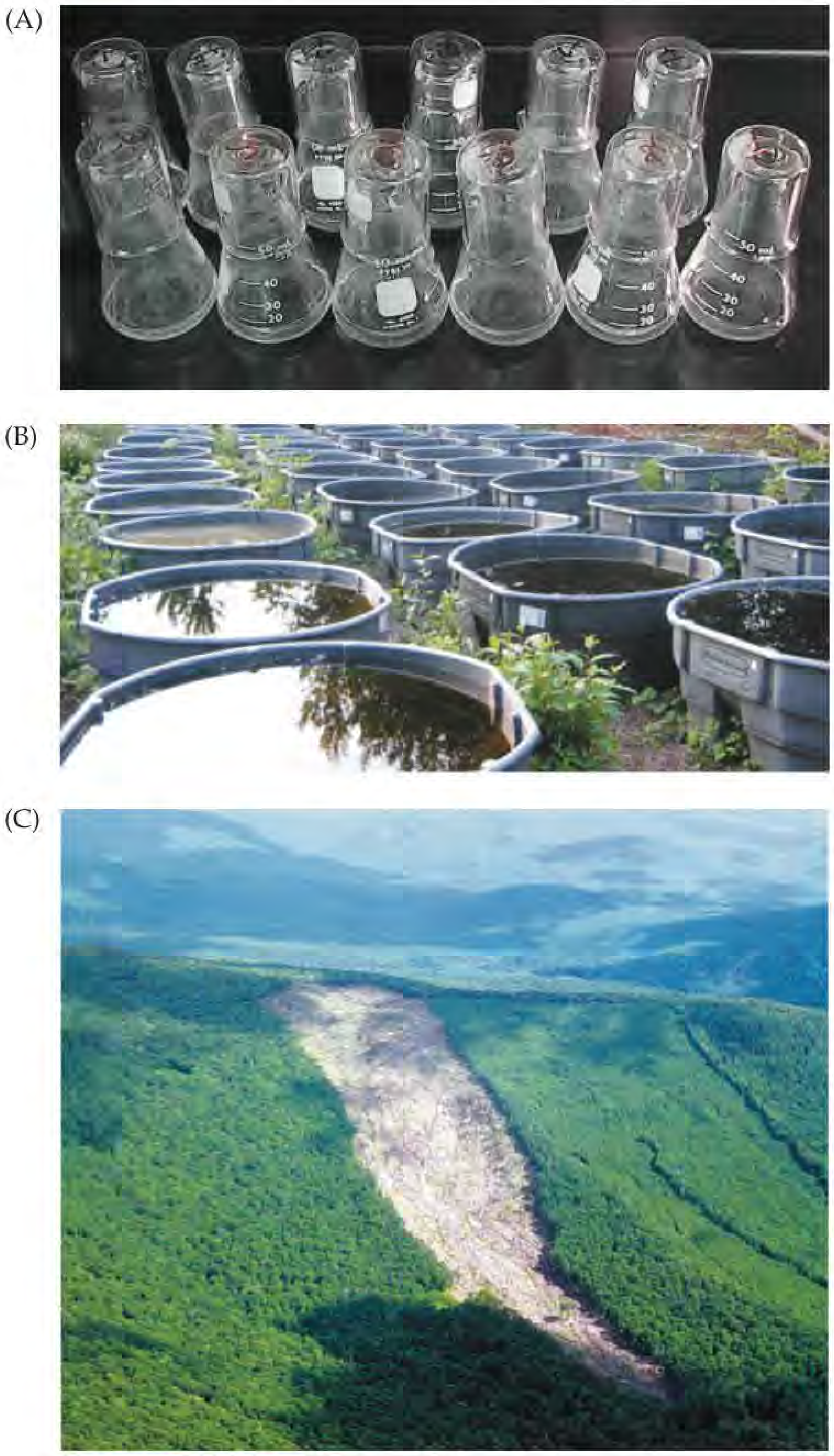


Figure 1.12 Ecological Experiments Experiments in ecology range from (A) laboratory experiments to (B) small-scale field experiments conducted in natural or artificial environments to (C) large-scale experiments that alter major components of an ecosystem, as seen in this clear-cut watershed. (A courtesy of Tim Cooper and Richard Lenski; B courtesy of Simone DesRoches and Dolph Schluter.)

with another. When possible, such experiments include both a control group (which is not subjected to alterations) and one or more experimental groups. When performing an experiment, ecologists have a range of types and scales to choose from, including laboratory studies, small-scale field studies that cover a few square meters, and large-scale field studies in which entire ecosystems, such as lakes or forests, are manipulated (**Figure 1.12**).

In some cases, however, it can be difficult or impossible to perform an appropriate experiment. For example, when ecologists are seeking to understand events that cover large geographic regions or occur over long periods, experiments can provide useful information, but they cannot provide convincing answers to the underlying questions of interest. As an example, let's consider global warming.

CLIMATE CHANGE CONNECTION

Approaches Used To Study Global Warming As we will see in Figure 25.11, temperature data show that Earth's climate is warming, but the future magnitude and effects of global warming remain uncertain. We are not sure, for example, how the geographic ranges of different species will change as a result of the projected temperature increases. There is only one Earth, so of course even if we wanted to, we could not apply different levels of global warming to copies of the planet and then observe how the ranges of species change over time in each of our experimental treatments.

Instead, we must approach such problems using a mixture of observational studies, experiments, and quantitative (mathematical or computer) approaches. Field observations reveal that many species have shifted their ranges poleward or up the sides of mountains in a manner that is consistent with the amount of global warming that has already occurred (Parmesan 2006). Field observations can also be used to summarize the environmental conditions under which species are currently found, and experiments can be used to examine the performance of species under different environmental conditions. To put all this information together, scientists can use results from observational studies and experiments to develop quantitative models that predict how the geographic ranges of species will change depending on how much the planet actually warms in the future.

The observation that global warming has already altered the geographic ranges of species brings us to a topic addressed in many chapters of this book: **climate change**. This term refers to a directional change in climate (such as global warming) that occurs over 3 decades or longer. As you'll read in later chapters, climate affects many aspects of ecology, such as the growth and survival of individuals, interactions between members of different species, and the relative abundances of species in ecological communities. These observations suggest that *changes* to climate may have far-reaching effects—and they do, as shown by the changes that have already occurred in the physiology, survival, reproduction, or geographic ranges of hundreds of species (Parmesan 2006). (See **Online Climate Change Connection 1.1** for further information on the ecological effects of climate change.)

Experiments are designed and analyzed in consistent ways

When ecologists perform experiments, they often take the three additional steps described in **Ecological Toolkit 1.1**: they replicate each treatment, they assign treatments

ECOLOGICAL TOOLKIT 1.1 Designing Ecological Experiments

A key step in any ecological experiment occurs well before it is performed: the experiment must be designed carefully. In a controlled experiment, an *experimental group*, which has the factor being tested, is compared with a *control group*, which does not. Different levels of the factor being tested are often referred to as different *treatments*. For example, in the experiment by Johnson et al. (1999) discussed earlier in this chapter, the control group received a treatment of 0 parasites per container, while members of the experimental group were assigned to one of three other treatments (16, 32, or 48 parasites per container).

The design of many ecological experiments includes three additional steps: *replication*, *random assignment of treatments*, and *statistical analyses*. Replication and random assignment of treatments are used to reduce the chance that variables not under the control of the experimenter will unduly influence the results of the experiment. Once the experiment has been completed, statistical analyses are used to assess the extent to which the results from the different treatments differ from one another.

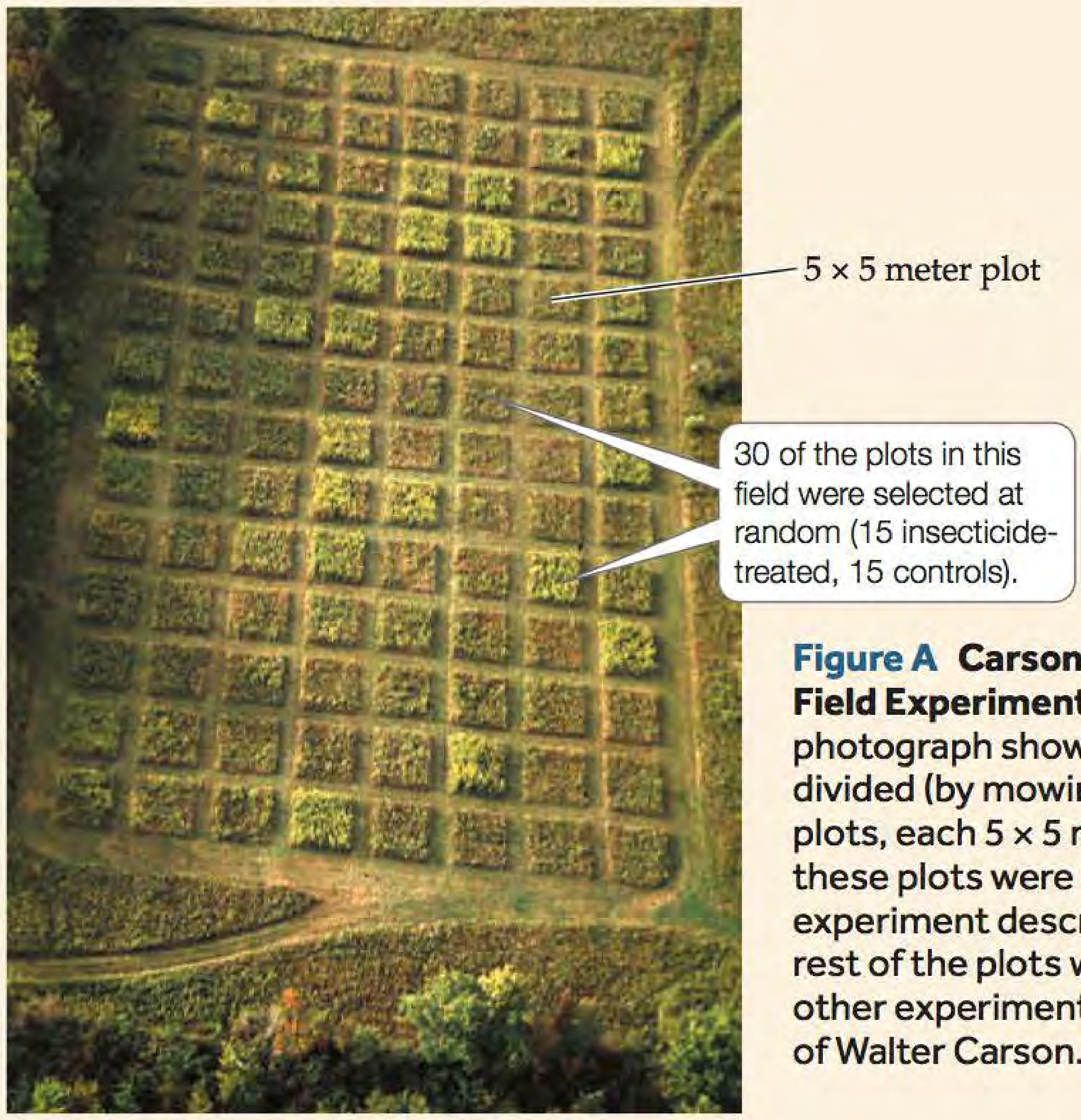


Figure A Carson and Root's Field Experiment This aerial photograph shows the field divided (by mowing) into 112 plots, each 5 × 5 m. Thirty of these plots were used in the experiment described here; the rest of the plots were used in other experiments. (Courtesy of Walter Carson.)

Several features of experimental design can be illustrated by the layout used in field studies performed by Richard B. Root and colleagues at Cornell University. In one such study, Carson and Root (2000) examined how herbivorous (plant-eating) insects affected a plant community dominated by the goldenrod *Solidago altissima*. Their first step was to define their research question: Does plant abundance, growth, or reproduction differ between insecticide-treated and control plots? To find out, they divided a field of goldenrods into the grid of 5 × 5 m plots shown in **Figure A**. The experiment ran for 10 years and used two treatments: a control, in which natural processes were left undisturbed, and an insect removal treatment, in which an insecticide was applied annually to reduce the numbers of herbivorous insects. Carson and Root selected 30 plots at random for use in the experiment; half of those plots were then selected at random to receive the insecticide treatment, while the remaining plots served as controls. Thus, there were 15 replicates for each treatment. Statistical analyses of the results indicated that herbivorous insects had major effects on the plant community, as is also suggested by the photograph in **Figure B**.

Figure B Carson and Root's Results A plot sprayed with insecticide (right) is shown surrounded by several control plots. (Courtesy of Walter Carson.)

at random, and they analyze the results using statistical methods.

Replication means that each treatment, including the control, is performed more than once. An advantage of replication is that as the number of replicates increases, it becomes less likely that the results are due to a variable that was not measured or controlled in the study. Imagine that Kiesecker had performed his field experiment with only two ponds, one with detectable levels of pesticides and the other without. Suppose he had found that frog deformities were more common in the single pond that contained pesticides. While pesticides might have been responsible for this result, the two ponds could have differed in many other ways, too, one or more of which might have been the real cause of the deformities. By using three ponds with pesticides and three ponds without pesticides, Kiesecker made it less likely that each of the three ponds with pesticides also contained something else—some variable not controlled in his experiment—that increased the chance of frog deformities. In his experiment, Kiesecker accounted for the possible effects of some uncontrolled variables: he showed, for example, that the number of snails and the frequency of their infection by *Ribeiroia* were similar in all six ponds, thus making it unlikely that the ponds with pesticides had many more *Ribeiroia* than the ponds without pesticides.

Ecologists also seek to limit the effects of unmeasured variables by assigning treatments at random. Suppose an investigator wanted to test whether insects that eat plants decrease the number of seeds the plants produce. One way to test this idea would be to divide an area into a series of plots (see Ecological Toolkit 1.1), some of which would be sprayed regularly with an insecticide (the experimental plots) while others would be left alone (the control plots). The decision as to whether a particular plot would be sprayed (or not) would be made at random at the start of the experiment. Assigning treatments at random would make it less likely that the plots that receive a particular treatment share other characteristics that might influence seed production, such as high or low levels of soil nutrients.

Finally, ecologists often use statistical analyses to determine whether their results are "significant." To understand why, let's turn again to Kiesecker's experiment. It would have been surprising if Kiesecker had found that rates of frog deformities in ponds with pesticides were exactly equal to those in ponds without pesticides. But how different would those rates have to be to show that the pesticides are having an effect? Since the results of different experimental treatments will rarely be identical, the investigator must ask whether an observed difference is great enough to be of biological importance. Statistical methods are often used as a standardized way to help make this decision. We describe general statistical principles and one statistical method, the *t*-test, in **Web Stats Review 2.2**. There are many different types of statistical analyses; books such as those by Zar (2009), Sokal and Rohlf (2011), and Gotelli and Ellison (2013) provide examples of which statistical methods to use under various circumstances.

What we know about ecology is always changing

The information in this book is not a static body of knowledge. Instead, like the natural world itself, our understanding of ecology is constantly changing. Like all scientists, ecologists observe nature and ask questions about how nature works. For example, when the existence of amphibian deformities became widely known in 1995, some scientists set out to answer a series of questions about those deformities. There were many things they wanted to know: How many species were afflicted by deformities? Did amphibian deformities occur in a few or many geographic regions? What caused the deformities, and did these causes differ among species or geographic regions?

The questions stimulated by the discovery of amphibian deformities illustrate the first in a series of four steps by which scientists can learn about the natural world. These four steps constitute the **scientific method**, which can be summarized as follows:

1. Observe nature and ask a well-framed question about those observations.
2. Use previous knowledge or intuition to develop possible answers to that question. In science, such possible explanations of a well-framed question are called **hypotheses**.
3. Evaluate competing hypotheses by performing experiments, gathering carefully selected observations, or analyzing results of quantitative models.
4. Use the results of those experiments, observations, or models to modify one or more of the hypotheses, to pose new questions, or to draw conclusions about the natural world.

This four-step process is iterative and self-correcting. New observations lead to new questions, which stimulate ecologists to formulate and test new ideas about how nature works. The results from such tests can lead to new knowledge, still more questions, or the abandonment of ideas that fail to explain the results. Although this four-step process is not followed exactly in all scientific studies, the back-and-forth between observations, questions, and results—potentially leading to a reevaluation of existing ideas—captures the essence of how science is done.

We've already seen some examples of how the process of scientific inquiry works: as answers to some questions about amphibian deformities were found, new questions arose, and new discoveries were made. You can explore one such discovery in **Analyzing Data 1.1**, which

ANALYZING DATA 1.1 Are Introduced Predators a Cause of Amphibian Decline?

Introduced predators are one of many factors thought to have contributed to amphibian population declines, although only a few studies have tested this hypothesis. In one such study, Vance Vredenburg* assessed the effects of two introduced fish species, the rainbow trout (*Oncorhynchus mykiss*) and the brook trout (*Salvelinus fontinalis*), on a frog species in decline, the mountain yellow-legged frog (*Rana muscosa*). Prior to any experimental manipulations, Vredenburg surveyed 39 lakes. For each lake, he noted whether introduced trout were present and then estimated frog abundance; the data from his survey include the following:

LAKE STATUS	AVERAGE FROG DENSITY (PER 10 M OF SHORELINE)
Trout absent	184.8
Trout present	15.3

Vredenburg then performed experiments in which he compared frog abundances in three categories of lakes: removal lakes (from which he removed introduced trout), fishless control lakes (that had never contained trout), and fish control lakes (that still contained trout). The data obtained from these experiments appear in the graph. Error bars show one SE of the mean.

1. From the survey data in the table, construct a bar graph showing the average density of frogs in lakes with and without trout (see **Web Stats Review 1.1.2** for a description of bar graphs). What can you conclude from these data? In your answer, distinguish between causation and correlation.
2. Explain why two types of control lakes were used in the experiment.
3. Consider the data for removal lakes 1, 2, and 3. For each of these lakes, calculate (a) the average number of frogs (per 10 m of shoreline) for the 1-year period that ends just before the time frame during which trout were removed and (b) the average number of frogs (per 10 m of shoreline) for the 1-year period that starts a year after the removal of trout began. What can you conclude from these calculations?
4. What do the survey and experimental results suggest about (a) the effect of introduced trout on amphibian populations and (b) prospects for population recovery once trout are removed?

See the companion website for a similar ANALYZING DATA exercise.

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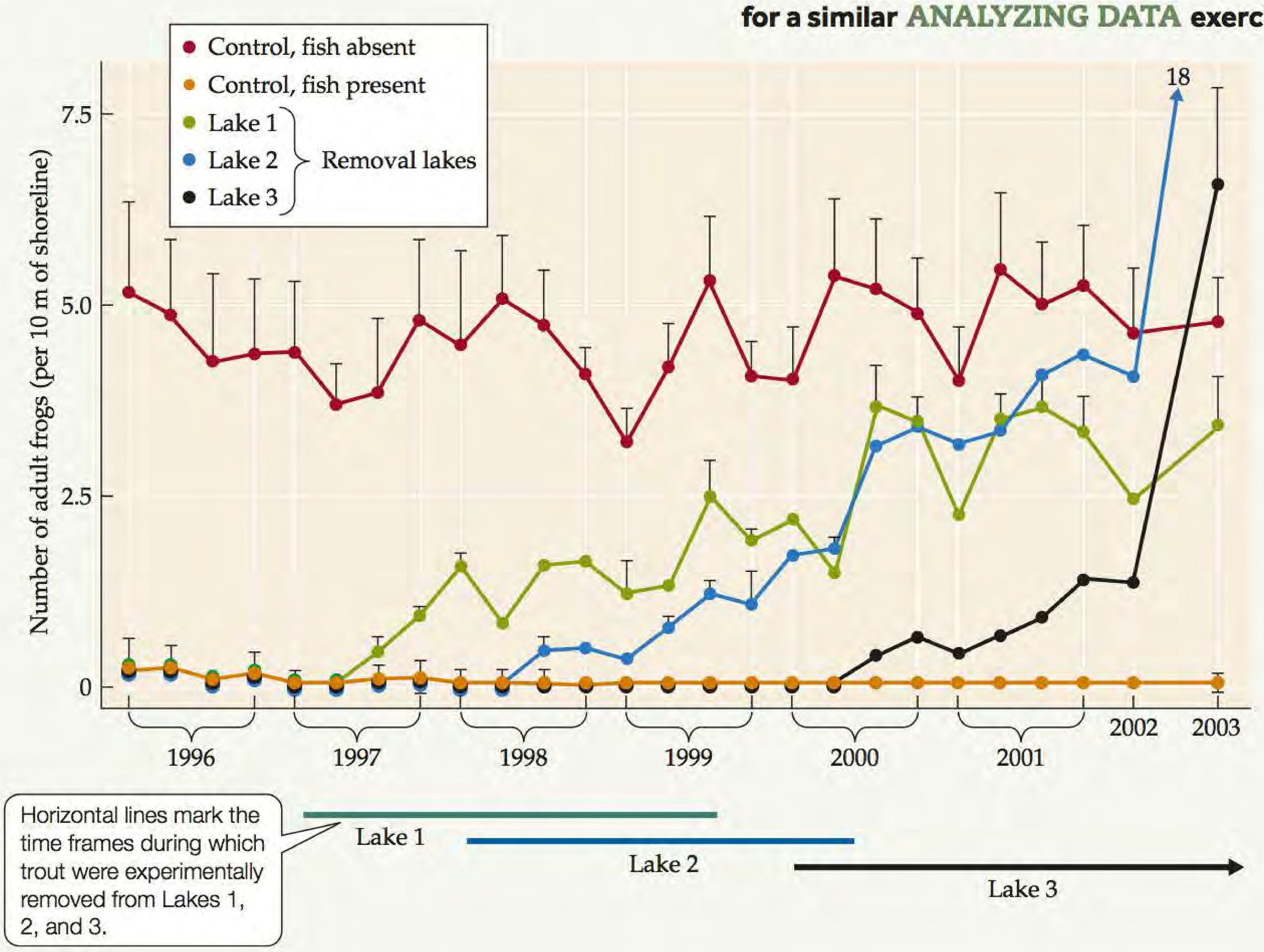
*Vredenburg, V. T. 2004. Reversing introduced species effects: Experimental removal of introduced fish leads to rapid recovery of a declining frog. *Proceedings of the National Academy of Sciences USA* 101: 7646–7650



Horizontal lines mark the time frames during which trout were experimentally removed from Lakes 1, 2, and 3.

examines whether introduced species can cause amphibian populations to decline. Indeed, new discoveries occur in all fields of ecology, suggesting that our understanding of ecological processes is, and always will be, a work in progress.

A CASE STUDY REVISITED

Deformity and Decline in Amphibian Populations

As we've seen in this chapter, amphibian deformities are often caused by parasites, but they can also be influenced by other factors, such as exposure to pesticides or fertilizers. Studies have also suggested that a range of factors can cause amphibian abundances to drop. Such factors include habitat loss, parasites and diseases, pollution, climate change, overexploitation, and introduced species.

A consensus has yet to be reached on the relative importance of these and other factors that affect amphibian declines. For example, Stuart et al. (2004) analyzed the results of studies on 435 amphibian species that have experienced rapid declines since 1980. Habitat loss was the primary cause of decline for the largest number of species (183 species), followed by overexploitation (50 species). The cause of decline for the remaining 207 species was listed as "enigmatic": populations of these species were declining rapidly for reasons that were poorly understood. Skerratt et al. (2007) argued that many such enigmatic declines were caused by pathogens such as the chytrid *Batrachochytrium dendrobatidis*, a fungus that causes a lethal skin disease. This conclusion has now been supported by many other studies (e.g., Voyles et al. 2009; Berger et al. 2016). Although the fungus continues to spread rapidly and has driven hundreds of amphibian populations to extinction, there are signs of hope. For example, McMahon et al. (2014) have shown that some amphibians can acquire resistance to *B. dendrobatidis* when exposed to live or dead fungus, while others have found evidence of resistance in wild populations (Eskew et al. 2015).

Other researchers have emphasized the importance of ongoing climate change. Hof et al. (2011), for example, project that by 2080, climate change will harm more amphibian species than will *B. dendrobatidis*. The impacts of factors such as disease and climate change are not mutually exclusive, however. Indeed, Rohr and Raffel (2010) found that while disease often led to amphibian declines, climate change (specifically, increased temperature variability) also played a key role. In particular, the impact of climate change on temperature variability appears to have decreased the resistance of frogs to *B. dendrobatidis* (Raffel et al. 2012).

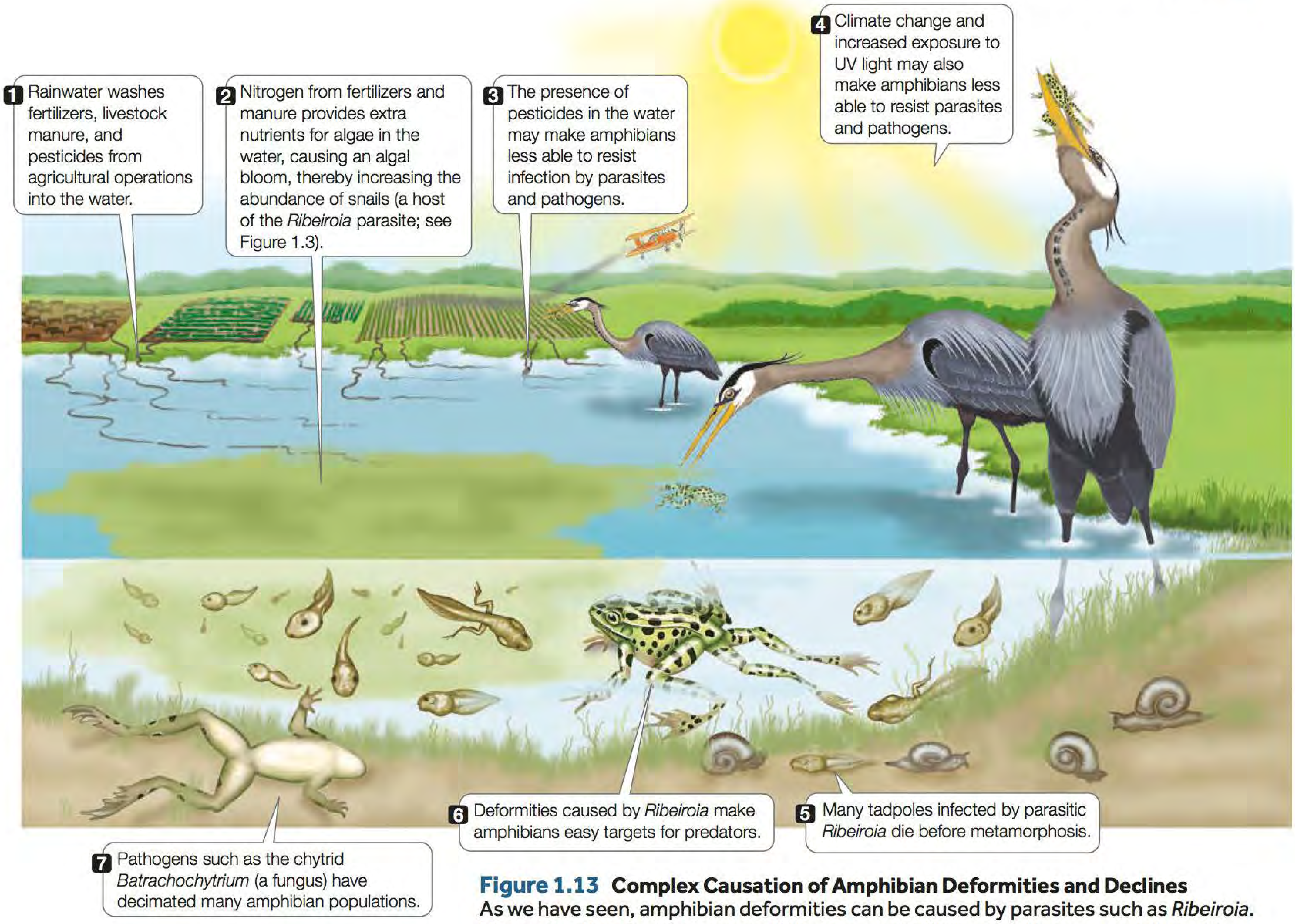
Collectively, these and other studies of amphibian population declines suggest that no single factor can explain most of them. Instead, the declines seem to be caused by complex factors that often act together and may vary from place to place. Consider, for example, the effects of pesticides. Although pesticides appear to increase the incidence of frog deformities, many studies have failed to link pesticides to decreases in the size of amphibian populations. However, many of these negative findings came from laboratory studies that held other factors constant and examined the effect of pesticides alone on amphibian growth or survival. Rick Relyea, of Rensselaer Polytechnic Institute, repeated such experiments, but with an added twist: predators. In two of six amphibian species studied, pesticides became up to 46 times more lethal if tadpoles sensed the presence of a predator (Relyea 2003). The predators were kept separate from the tadpoles by netting, but the tadpoles could smell them.

In Relyea's experiments, the ability of some tadpoles to cope with pesticides was reduced by stress caused by the presence of a predator. The mechanism by which these two factors act together is unknown. In general, although we know that a broad set of factors can cause frog deformities and declines (**Figure 1.13**), relatively little is known about the extent to which these factors interact or how any such interactions exert their effects. In this and many other areas of ecology, we have learned enough to solve parts of the mystery, yet more remains to be discovered.

CONNECTIONS IN NATURE

Mission Impossible?

As we emphasized in the opening pages of this chapter, people have begun to realize that it is important for us to understand how nature works, if only to protect ourselves from inadvertently changing our environment in ways that cause us harm. Does the fact that the natural world is vast, complex, and interconnected mean that it is impossible to understand? Most ecologists do not think so. Our understanding of natural systems has improved greatly in the last 100 years. Ongoing efforts to understand how nature works are sure to be challenging, but such efforts are also enormously exciting and important. What we learn, and how we use that knowledge, will have a great impact on the current and future well-being of human societies. Whatever your career path, we hope this book will help you understand the natural world in which you live, as well as how you affect—and are affected by—that world.



1 Rainwater washes fertilizers, livestock manure, and pesticides from agricultural operations into the water.

2 Nitrogen from fertilizers and manure provides extra nutrients for algae in the water, causing an algal bloom, thereby increasing the abundance of snails (a host of the *Ribeiroia* parasite; see Figure 1.3).

3 The presence of pesticides in the water may make amphibians less able to resist infection by parasites and pathogens.

4 Climate change and increased exposure to UV light may also make amphibians less able to resist parasites and pathogens.

5 Many tadpoles infected by parasitic *Ribeiroia* die before metamorphosis.

6 Deformities caused by *Ribeiroia* make amphibians easy targets for predators.

7 Pathogens such as the chytrid *Batrachochytrium* (a fungus) have decimated many amphibian populations.

Figure 1.13 Complex Causation of Amphibian Deformities and Declines As we have seen, amphibian deformities can be caused by parasites such as *Ribeiroia*. However, other factors—many of them a result of human actions—may interact to cause amphibian deformities and declines. (After Blaustein and Johnson 2003.)

Summary

CONCEPT 1.1 Events in the natural world are interconnected.

- Laboratory and field experiments on the effects of parasites on amphibian deformities illustrate how events in nature can be connected with one another.
- Because events in the natural world are interconnected, any action can have unanticipated side effects.
- People both depend on and affect the natural environment.

CONCEPT 1.2 Ecology is the scientific study of interactions between organisms and their environment.

- Ecology is a scientific discipline that is related to, but differs from, disciplines such as environmental science.
- Public and professional ideas about ecology often differ.
- Ecology is broad in scope and encompasses studies at many levels of biological organization.
- All ecological studies address events on some spatial and temporal scales while ignoring events at other scales.

CONCEPT 1.3 Ecologists evaluate competing hypotheses about natural systems with observations, experiments, and models.

- In an ecological experiment, an investigator alters one or more features of the environment and observes the effect of that change on natural processes.
- Some features of the natural world are best investigated with a combination of field observations, experiments, and quantitative models.
- Experiments are designed and analyzed in consistent ways: typically, each treatment, including the control, is replicated; treatments are assigned at random; and statistical methods are used to analyze the results.
- The information in this book is not a static body of knowledge; what we know about ecology is always changing.

Review Questions

1. Describe what the phrase "connections in nature" means, and explain how such connections can lead to unanticipated side effects. Illustrate your points with an example discussed in the chapter.
2. What is ecology, and what do ecologists study? If an ecologist studied the effects of a particular gene, describe how the emphasis of that researcher's work might differ from the emphasis of a geneticist or cell biologist.
3. How does the scientific method work? Include in your answer a description of a controlled experiment.

ON THE COMPANION WEBSITE

ecology4e.sinauer.com

The website includes companions to all of the Analyzing Data exercises, Online Quizzes, Flashcards, Suggested Readings, and more. In addition, the following resources are available for this chapter:

Hands-On Problem Solving

1.1 When a Mosquito Flaps Its Wings...: Connections in the Natural World

Online Climate Change Connection

1.1 Ecological Effects of Climate Change

Hone Your Problem-Solving Skills

Twenty tadpoles of a certain frog species, 15 adult snails (collected from ponds containing deformed frogs), and identical amounts of phytoplankton (small algae that grow suspended in water) and attached algae (that grow on rocks) were added to each of 10 freshwater tanks. Atrazine (an herbicide that is often found in ponds) was added to 5 of these tanks; no atrazine was added to the other 5 tanks. After 6 months, the mean values shown in the table were determined for phytoplankton abundance, attached algae abundance, water clarity (measured on a scale of 1–5, where 1 is most cloudy and 5 is mostly clear), number of tadpole eosinophils (a type of white blood cell used in the tadpole's immune response), tadpole survival, and number of cysts of the trematode parasite *Ribeiroia*.

	TREATMENT	
VARIABLE	ATRAZINE ADDED	NO ATRAZINE
Phytoplankton (abundance index)	2.1	6.4
Attached algae (abundance index)	1.4	0.9
Water clarity (scale 1–5)	4.9	3.8
Eosinophils (number/ml blood)	1.2	2.7
Tadpole survival (%)	45	72
Ribeiroia cysts (number/tadpole)	28.6	6.9

1. Identify the control used in this experiment. How would investigators use the controls to help them interpret experimental results?
2. Describe the results for phytoplankton abundance, attached algae abundance, and water clarity. Interpret these results.
3. Describe the results for eosinophil number, tadpole survival, and number of *Ribeiroia* cysts. Interpret these results.
4. Based on the results in the table and the *Ribeiroia* life cycle (see Figure 1.3), describe a chain of events that could affect a frog population after atrazine was added to a pond.

Unit 1

Organisms and Their Environment

2

The Physical Environment

KEY CONCEPTS

CONCEPT 2.1 Climate is the most fundamental component of the physical environment.

CONCEPT 2.2 Winds and ocean currents result from differences in solar radiation across Earth's surface.

CONCEPT 2.3 Large-scale atmospheric and oceanic circulation patterns establish global patterns of temperature and precipitation.

CONCEPT 2.4 Regional climates reflect the influence of oceans and continents, mountains, and vegetation.

CONCEPT 2.5 Seasonal and long-term climate variation are associated with changes in Earth's position relative to the sun.

CONCEPT 2.6 Salinity, acidity, and oxygen concentrations are major determinants of the chemical environment.

Climate Variation and Salmon Abundance: A Case Study

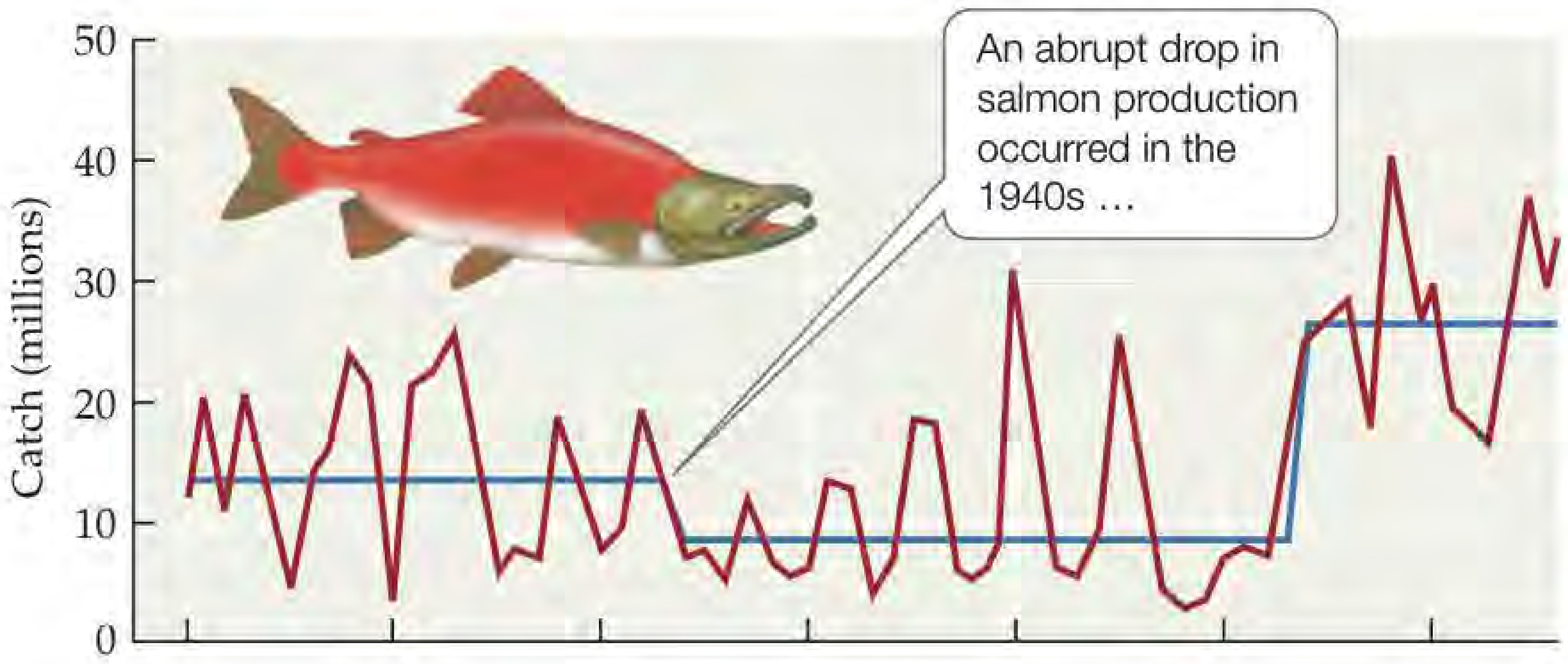
Grizzly bears of the Pacific Northwest feast seasonally on the salmon that arrive in huge numbers to reproduce in the streams of the region (**Figure 2.1**). Salmon are *anadromous*; that is, they are born in freshwater streams, spend their adult lives in the ocean, and then return to spawn in the freshwater habitats where they were born. Grizzlies capitalize on the salmon's reproductive habits, gorging themselves on this rich food resource. These normally aggressive bears will forgo their usual territorial behavior and tolerate high densities of other bears while fishing for salmon.

It is not only bears that rely on salmon for food. Salmon have been an important part of the human economy of the Pacific Northwest for millennia. The fish were a staple of the diets of Native Americans in this region as well as a central part of their cultural and spiritual lives. Salmon are now fished commercially in the waters of the North Pacific Ocean, providing a $3 billion economic base for coastal communities across the North Pacific. Commercial salmon fishing is a risky venture, however. Successful reproduction for salmon depends on the health of the streams in which they spawn. The construction of dams, increased stream sediments due to forest clear-cutting, water pollution, and overharvesting have all been blamed for declines in salmon populations, primarily from the California coast northward to British Columbia (Walters 1995). Despite efforts to mitigate this environmental degradation, the recovery of salmon stocks has been marginal at best in the southern portion of the region.

Researchers, environmental advocates, and government policy experts have focused primarily on the deterioration of freshwater habitat as a cause for the declines in salmon. In 1994, however, Steven Hare and Robert Francis at the University of Washington suggested that changes in the marine environment, where salmon spend the majority of their adult lives, could be contributing to the declines in salmon abundance. In particular, they noted that records of fish harvests covering more than a century indicated that multi-decadal periods of low or high fish production have occurred repeatedly, separated by abrupt changes in production rather than gradual transitions (**Figure 2.2**). In addition, Nathan Mantua and colleagues (Mantua et al. 1997) noted that periods of high salmon production in Alaska corresponded with periods of low salmon production at the southern end of the salmon range, particularly in Oregon and Washington. They found telling quotes in commercial fishing publications that told the same story: when the fishing was poor in Washington and Oregon, it was good in Alaska, and vice versa.

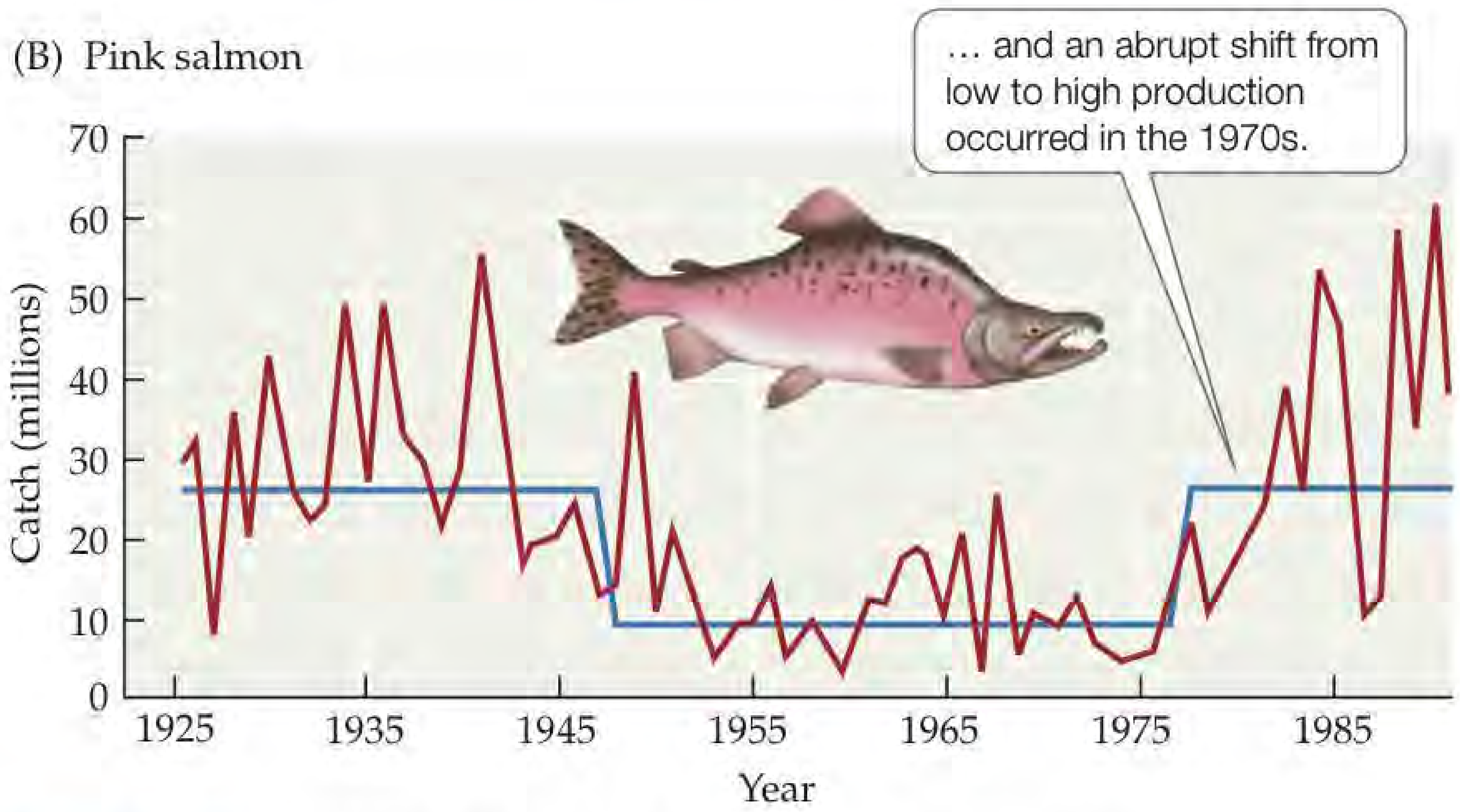
Figure 2.1 A Seasonal Opportunity Grizzly bears feed on salmon migrating upstream in streams and rivers in Alaska to reproduce. The size of the salmon run each year depends in part on physical conditions in the Pacific Ocean, many miles away.

(A) Sockeye salmon



An abrupt drop in salmon production occurred in the 1940s …

(B) Pink salmon



… and an abrupt shift from low to high production occurred in the 1970s.

Figure 2.2 Changes in Salmon Harvests over Time Records of commercial harvests of (A) sockeye salmon and (B) pink salmon in Alaska over 65 years show abrupt drops and increases in production. Red lines represent annual catch; purple lines are a statistical fit to the data. (After Hare and Francis 1994.)

> From *Pacific Fisherman* (published in 1915):
>
> "Never before have the Bristol Bay [Alaska] salmon packers returned to port after the season's operations so early." [That is, it was a bad year, with few fish to catch.]
>
> "The spring [chinook salmon] fishing season on the Columbia River [Washington and Oregon] closed at noon on August 25, and proved to be one of the best for some years."
>
> From *Pacific Fisherman* (1939):
>
> "The Bristol Bay Red [Alaska sockeye salmon] run was regarded as the greatest in history."
>
> "The [chinook] catch this year is one of the lowest in the history of the Columbia [Washington]."

Hare and Francis hypothesized that the abrupt shifts in salmon production were associated with long-term climate variation in the North Pacific. The nature and cause(s) of these underlying climate shifts, however, were unclear. Additional work by Mantua and colleagues found good correspondence between the multi-decadal shifts in salmon production and changes in sea surface temperatures in the North Pacific.

How widespread is this variation in climate and its effects on salmon and the associated marine ecosystem? As we will see at the end of this chapter, the research on variation in salmon production led to the discovery of an important long-term cyclic climate pattern that affects a large area.

Introduction

The physical environment is the ultimate determinant of where organisms can live, the resources that are available to them, and the rate at which their populations can grow. Therefore, an understanding of the physical environment is key to understanding all ecological phenomena, from the outcome of interactions between bacteria and fungi in the soil to the exchange of carbon dioxide between the biosphere and the atmosphere.

The physical environment includes climate, which consists of long-term trends in temperature, wind, and precipitation. Radiation from the sun ultimately drives the climate system as well as biological energy production. Another aspect of the physical environment is the chemical composition of air and water, which includes salinity (concentrations of dissolved salts), acidity, and concentrations of gases in the atmosphere and dissolved in water. Soil is an important component of the physical environment because it is a medium in which microorganisms, plants, and animals live. Soil also influences the availability of critical resources, particularly water and nutrients. This chapter will focus on climate and the chemical environment; we will cover soil development and nutrient supply in Chapter 22.

This chapter will provide a framework for characterizing the physical environment, including its variability, at a variety of spatial and temporal scales. We will begin by exploring the processes that create the climate patterns we see at global to regional scales.

CONCEPT 2.1
Climate is the most fundamental component of the physical environment.

Climate

Each day we experience the **weather** around us: the current temperature, humidity, precipitation, wind, and cloud cover. Weather is an important determinant of our behavior: what we wear, the activities we engage in, and our mode of transportation. **Climate** is the long-term description of weather at a given location, based on averages and variation measured over decades. Climate variation includes the daily and seasonal cycles associated with

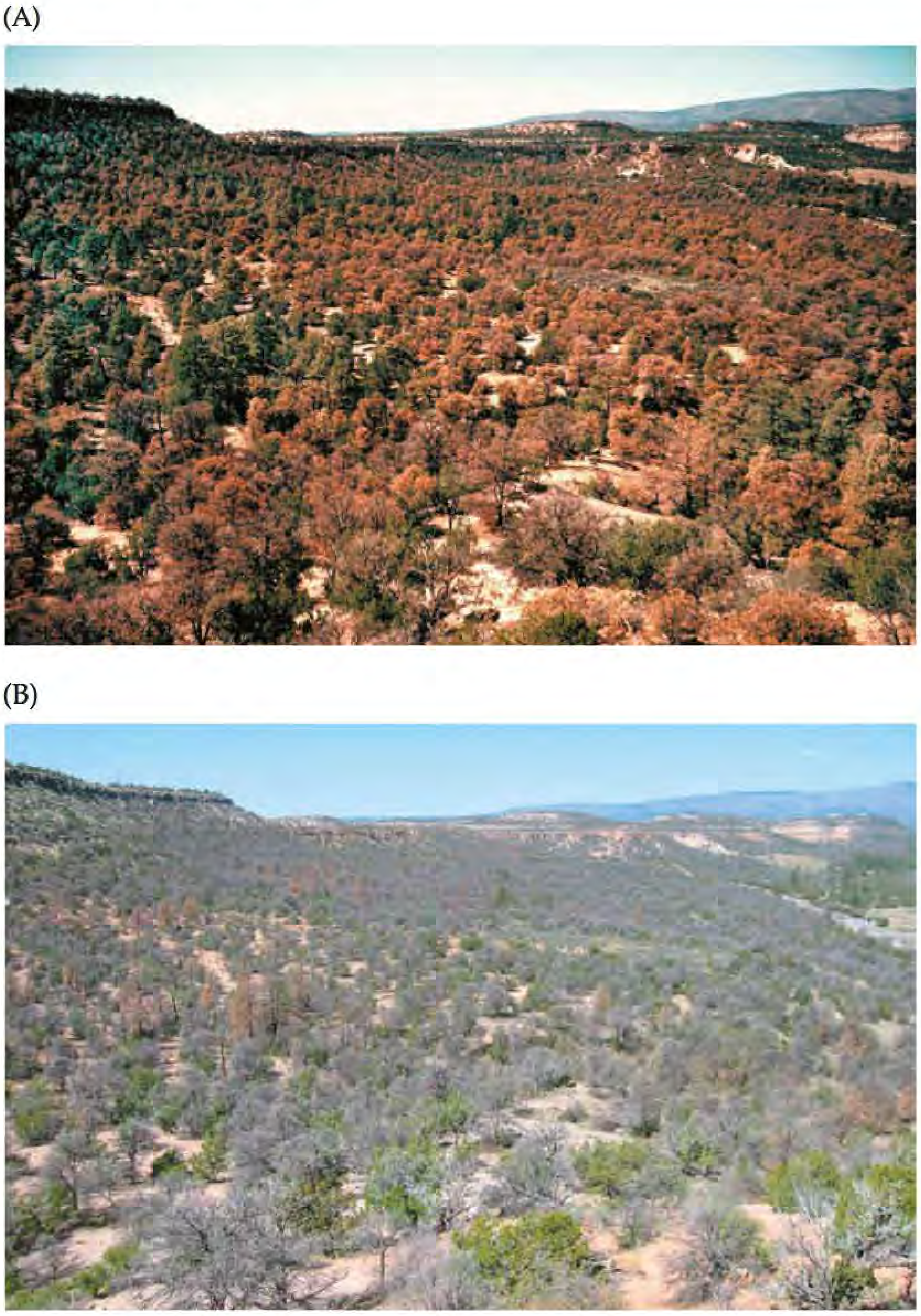


Figure 2.3 Widespread Mortality in Piñon Pines Extreme high temperatures and a historic drought from 2000 to 2003 killed large areas of piñon pines (*Pinus edulis*) throughout the southwestern United States. (A) Here, stands in the Jemez Mountains, New Mexico, begin to show substantial needle death due to water and temperature stress, combined with a bark beetle outbreak in October 2002. (B) By May 2004, most of the trees had died. (Courtesy of Craig Allen.)

changes in solar radiation as Earth rotates on its axis and orbits the sun. Climate variation also includes changes over years or decades, such as large-scale cyclic weather patterns related to changes in the atmosphere and oceans (the El Niño Southern Oscillation, discussed later in this chapter, is one example). Longer-term climate change occurs as a result of changes in the intensity and distribution of solar radiation reaching Earth's surface, as well as changes in the overall energy balance. Earth's climate is currently changing because of increases in concentrations of gases such as carbon dioxide that are emitted into the atmosphere as a result of human activities. These gases absorb energy and radiate it back to the surface, creating a greenhouse effect.

Climate controls where and how organisms live

Where organisms live, their geographic distribution, and how they function are determined by climate. Temperature determines the rates of biochemical reactions and physiological activity for all organisms. Water supplied by precipitation is an essential resource for terrestrial organisms. Freshwater organisms are dependent on precipitation for the maintenance and quality of their habitats. Marine organisms depend on ocean currents that influence the temperature and chemistry of the waters they live in.

We usually characterize climate—or any aspect of the physical environment—at a given location by the average conditions. However, the geographic distributions of organisms are influenced by *extreme* conditions more than average conditions because extreme events are important determinants of mortality. Temperature and moisture extremes can affect even long-lived organisms such as forest trees. For example, record high temperatures, along with a severe drought in 2000–2003, contributed to widespread mortality in large stands of piñon pines (*Pinus edulis*) in the southwestern United States (Breshears et al. 2005) (**Figure 2.3**). These long-lived plants could no longer survive in the region where they had existed for centuries. Thus, the physical environment must also be characterized by its *variability* over time, not just by average conditions, if we are to understand its ecological importance. The frequency and severity of extreme temperature events are predicted to increase in association with global climate change (Jentsch et al. 2007). These events will increase the probability of large-scale mortality of vegetation such as the die-off in piñon pines (see **Online Climate Change Connection 2.1**).

The *timing* of changes in the physical environment is also ecologically important. The seasonality of rainfall, for example, is important in determining the availability of water for terrestrial organisms. In regions with a "Mediterranean-type" climate, the majority of precipitation falls in winter. Although these regions receive more precipitation than most desert areas, they experience regular dry periods during summer. Lack of water during summer limits the potential growth of plants and promotes fires. In contrast, some grasslands have the same *average annual temperature* (the average temperature measured over an entire year) and precipitation as these Mediterranean-type ecosystems, but precipitation during the summer is higher.

Climate also influences the rates of abiotic processes that affect organisms. The rate at which rocks and soil are broken down to supply nutrients to plants and microorganisms, for example, is determined by climate. Climate can also influence the rates of periodic *disturbances*, such as fires, floods, and avalanches. These events kill organisms and disrupt biological communities, but they subsequently create opportunities for the establishment and growth of new organisms and communities.

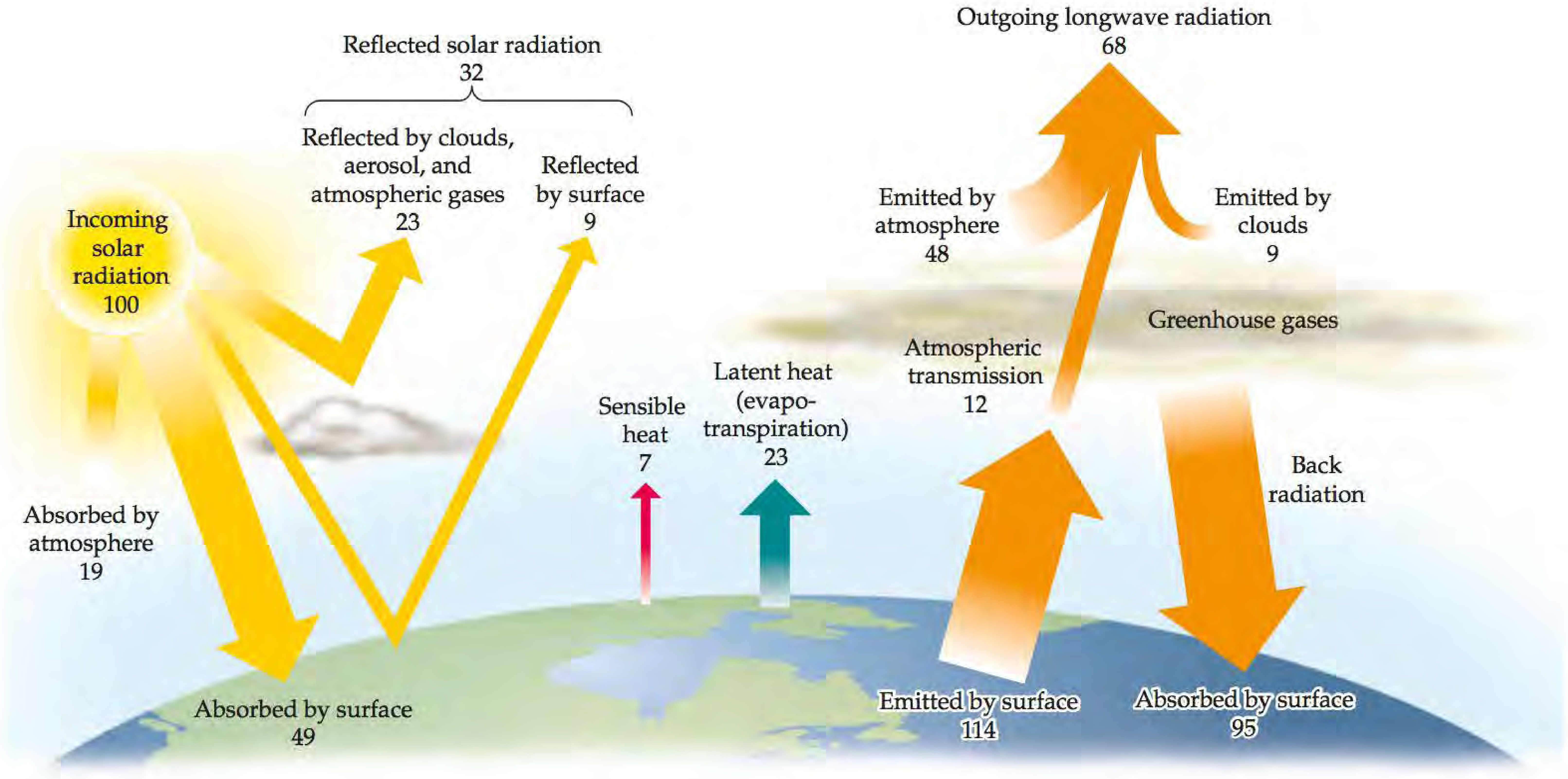


Figure 2.4 Earth's Energy Balance Average annual energy balance for Earth's surface and atmosphere, including gains from solar radiation and gains and losses due to emission of infrared radiation, latent heat flux, and sensible heat flux. The numbers are gains and losses of energy, given as percentages of the average annual incoming solar radiation at the top of Earth's atmosphere (342 W/m^2). (After Kiehl and Trenberth 1997.)

? What component of Earth's energy balance would be influenced by an increase in greenhouse gases? What would the effect on Earth's energy balance be if there were an increase in atmospheric aerosols?

Global energy balance drives the climate system

The energy that drives the global climate system is ultimately derived from solar radiation. On average, the top of Earth's atmosphere receives 342 watts (W) of solar radiation per square meter each year. About a third of this solar radiation is reflected back out of the atmosphere by clouds, fine atmospheric particles called *aerosols*, and Earth's surface. Another fifth of the incoming solar radiation is absorbed by ozone, clouds, and water vapor in the atmosphere. The remaining half is absorbed by land and water at Earth's surface (**Figure 2.4**).

If Earth's temperature is to remain the same, these energy gains from solar radiation must be balanced by energy losses. Much of the solar radiation absorbed by Earth's surface is emitted to the atmosphere as infrared radiation (also known as *longwave* radiation). Earth's surface also loses energy and is cooled when water evaporates, because the change in phase from liquid water to water vapor absorbs energy. Heat loss due to evaporation is known as **latent heat flux**. Energy is also transferred through the exchange of kinetic energy by molecules in direct contact with one another (**conduction**) and by the movement of currents of air (wind) and water (**convection**). Energy transfer from the warm air immediately above Earth's surface to the cooler atmosphere by convection and conduction is known as **sensible heat flux**.

The atmosphere absorbs much of the infrared radiation emitted from Earth's surface (and from clouds) and reradiates it back to Earth's surface. This reradiation represents a major energy gain. The atmosphere contains several gases, known as **greenhouse gases**, that absorb and reradiate infrared radiation. These gases include water vapor (H_2O), carbon dioxide (CO_2), methane (CH_4), and nitrous oxide (N_2O). Some of these greenhouse gases are produced through biological activity (e.g., CO_2, CH_4, N_2O), linking the biosphere to the climate system. Without these greenhouse gases, Earth's climate would be considerably cooler than it is (by approximately 33°C, or 59°F). As noted earlier, increases in atmospheric concentrations of greenhouse gases due to human activities are altering Earth's energy balance, changing the climate system, and causing global climate change (see Concept 25.2).

Our discussion of Earth's energy balance has focused on average annual transfers of energy to and from Earth as a whole. But not every location on Earth receives the same amount of energy from the sun. Let's consider how these differences in solar radiation affect the circulation of Earth's atmosphere and ocean waters.

CONCEPT 2.2

Winds and ocean currents result from differences in solar radiation across Earth's surface.

Atmospheric and Oceanic Circulation

It's hot near the equator and cold at the poles. Why is this true, and how does it relate to global climate patterns? Near the equator, the sun's rays strike Earth's surface perpendicularly. Toward the North and South Poles, the angle of the sun's rays becomes steeper, so the same amount of energy is spread over a progressively larger area of Earth's surface (**Figure 2.5**). In addition, the amount of atmosphere the rays must pass through increases toward the poles, so more radiation is reflected or absorbed before it reaches the surface. As a result, more solar energy is received per unit of area in the tropics (between 23.5° north and south latitudes) than in regions closer to the poles. This differential input of solar radiation not only establishes latitudinal gradients in temperature, but also is the driving force for climate dynamics such as warm and cold fronts and large storms (e.g., hurricanes). In addition, the movement of Earth around the sun, in combination with the tilt of Earth's axis of rotation, results in changes in the amount of solar radiation received at any location over the course of the year, as we'll see in Concept 2.5. These changes are the cause of seasonal climate variation: winter–spring–summer–fall changes at high latitudes and wet–dry shifts in tropical regions.

Atmospheric circulation cells are established in regular latitudinal patterns

A surface warmed by the sun emits infrared radiation and warms the air above it. As we have just seen, the heating of Earth's surface varies with latitude, and it can also vary with topography. Such differential warming creates pockets of warm air surrounded by cooler air. Warm air is less dense (has fewer molecules per unit of volume) than cool air, so as long as a pocket of air remains warmer than the surrounding air, it will rise (a process called **uplift**) (**Figure 2.6**). **Atmospheric pressure** is the force exerted by molecules of air on the air and surface below it. This pressure decreases with increasing altitude, so as a pocket of warm air rises, it expands. This expansion cools the rising air. Cool air cannot hold as much water vapor as warm air, so as the air continues to rise and cool, the water vapor contained within it begins to condense into droplets and form clouds.

The condensation of water into clouds is a warming process (another form of latent heat flux), which may act to keep the pocket of air warmer than the surrounding atmosphere and enhance its uplift, despite its cooling due to expansion. You may have observed this process on a warm summer day when bubble-shaped cumulus clouds formed thunderstorms. When there is substantial heating of Earth's surface and a progressively cooler atmosphere above the surface, the uplifted air will form clouds with wedge-shaped tops. The clouds reach to the boundary between the *troposphere*, the atmospheric layer above Earth's surface, and the *stratosphere*, the next atmospheric layer above the troposphere. This boundary is marked by a transition from progressively cooler temperatures in the troposphere to warmer temperatures in the stratosphere. Thus, the air pocket ceases to rise once it reaches the warmer temperatures at the boundary of the stratosphere.

Differential heating and storm formation explain why the tropics receive the most precipitation of any area on Earth. The tropics receive the most solar radiation and thus experience the greatest amount of surface heating, uplift of air, and cloud formation. The uplift of air in the tropics creates a band of low atmospheric pressure

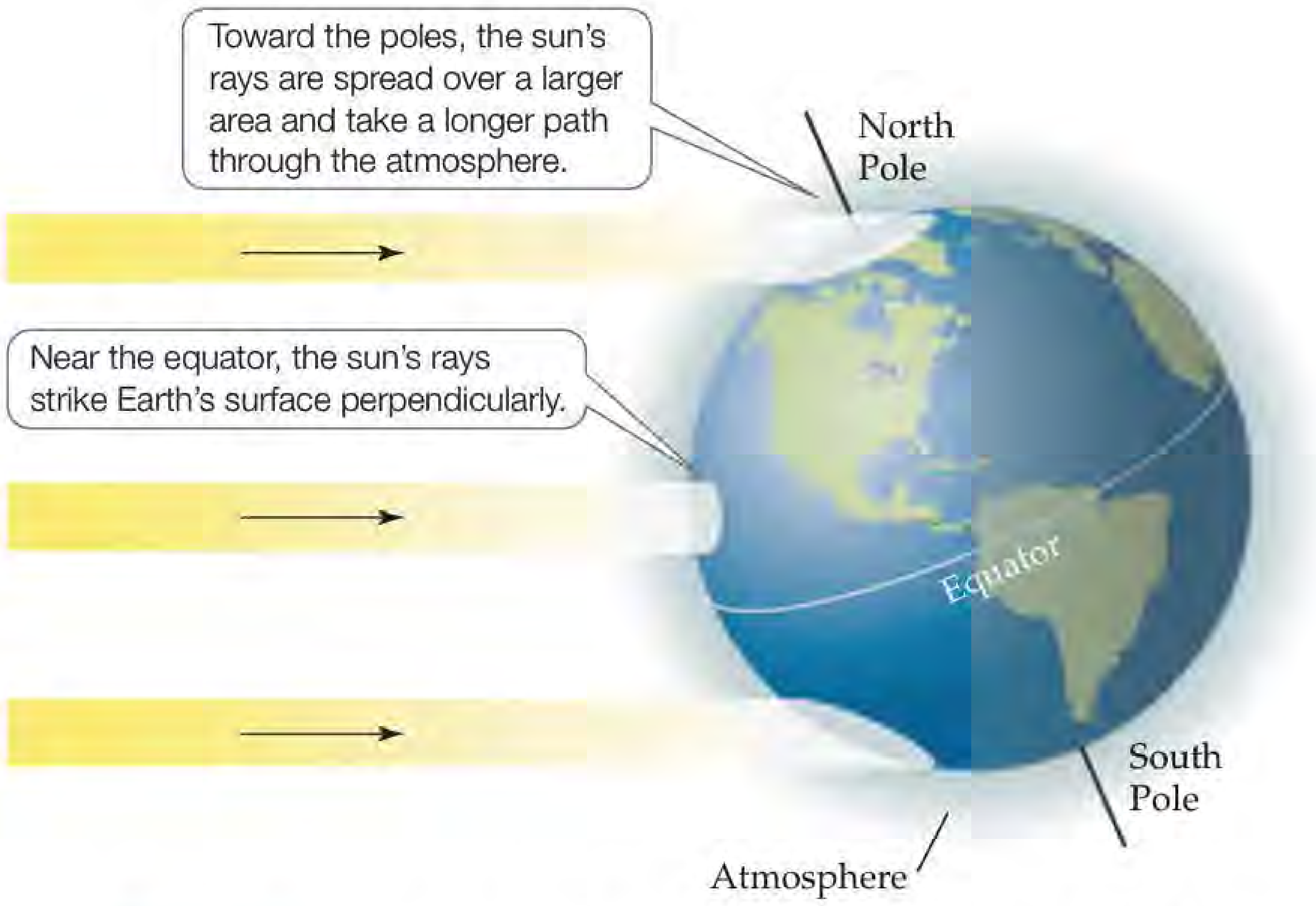


Figure 2.5 Latitudinal Differences in Solar Radiation at Earth's Surface The angle of the sun's rays affects the intensity of the solar radiation that strikes Earth's surface.

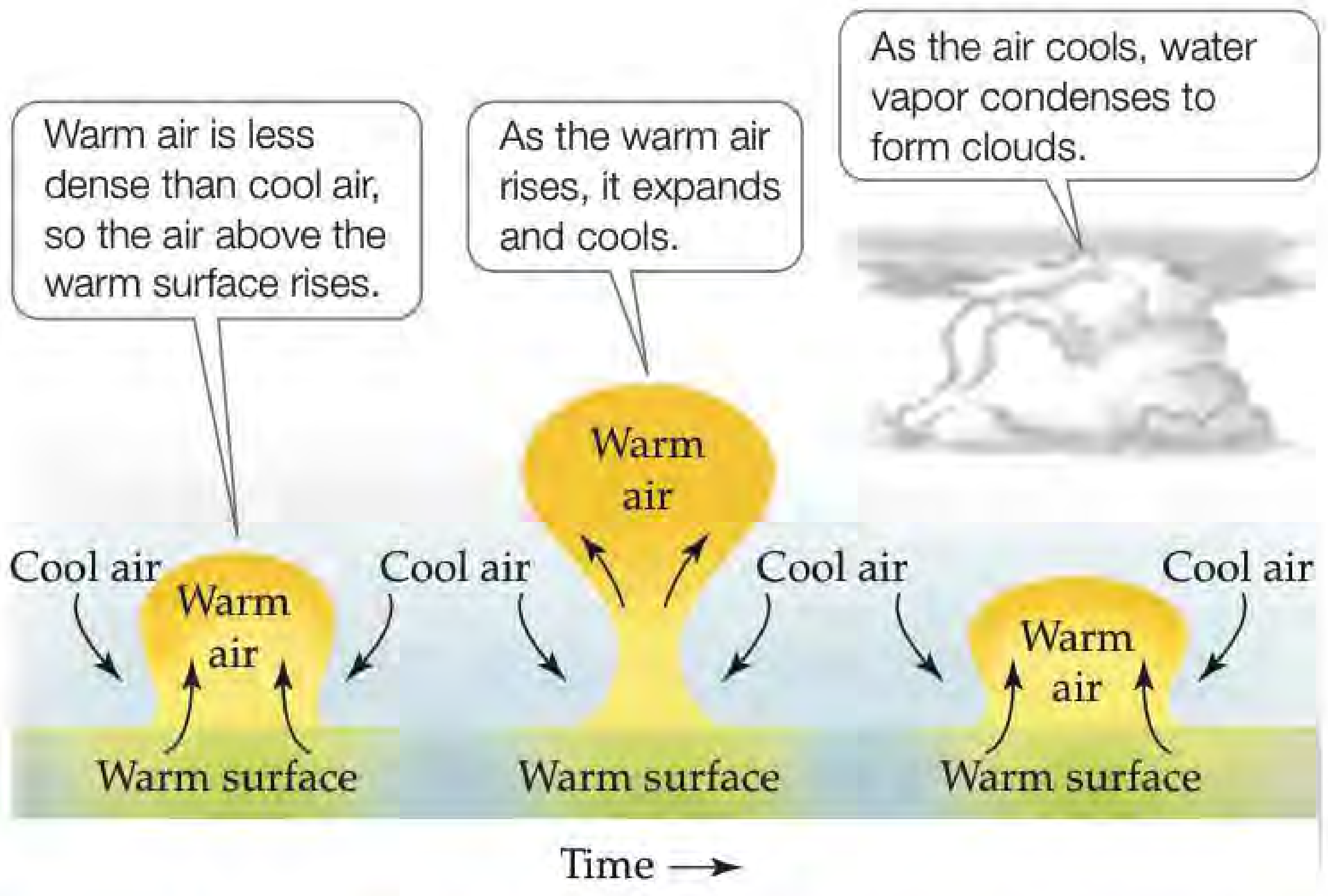


Figure 2.6 Surface Heating and Uplift Differential solar heating of Earth's surface leads to the uplift of pockets of air over the warmest surfaces.

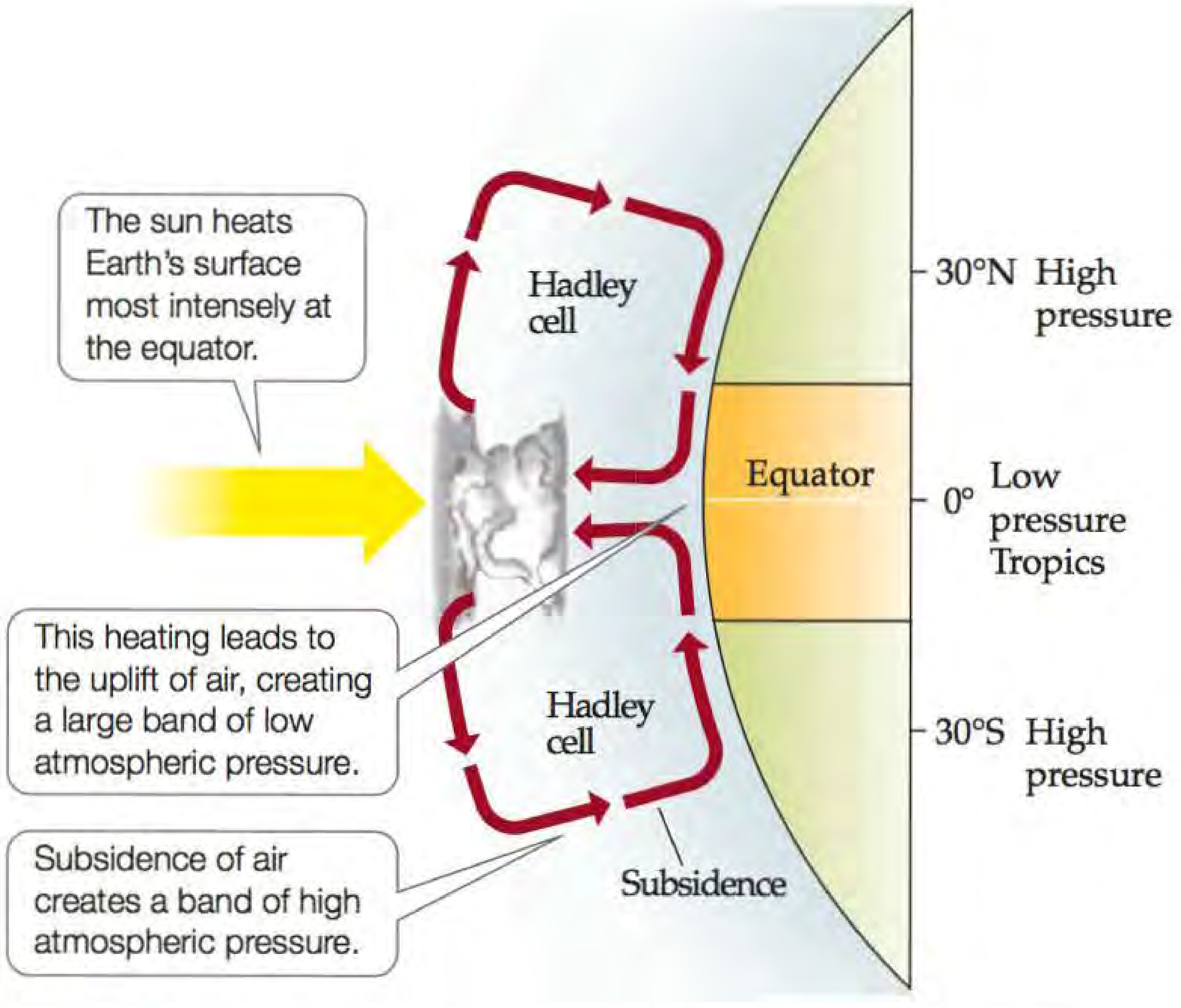


Figure 2.7 **Tropical Heating and Atmospheric Circulation Cells** The heating of Earth's surface in the tropics causes air to rise and release precipitation.

relative to zones to the north and south. When air rising over the tropics reaches the boundary between the troposphere and stratosphere, it flows toward the poles (**Figure 2.7**). Eventually, this poleward-moving air cools as it exchanges heat with the surrounding air and meets cooler air moving from the poles toward the equator. Once the air reaches a temperature similar to that of the surrounding atmosphere, it descends toward Earth's surface, a process known as **subsidence**. Subsidence creates regions of high atmospheric pressure around latitudes 30°N and S, which inhibit the formation of clouds, and Earth's major deserts are found at these latitudes.

The tropical uplift of air creates a large-scale pattern of atmospheric circulation in each hemisphere known as a **Hadley cell**, named after George Hadley, the eighteenth-century British meteorologist and physicist who first proposed its existence. Additional atmospheric circulation cells are formed at higher latitudes (**Figure 2.8**). The **polar cell**, as its name indicates, occurs at the North and South Poles. Cold, dense air subsides at the poles and moves toward the equator when it reaches Earth's surface. The descending air at the poles is replaced by air moving through the upper atmosphere from lower latitudes. Subsidence at the poles creates an area of high pressure, so the polar regions, despite the abundance of ice and snow on the ground, actually receive little precipitation and are known as polar deserts. An intermediate **Ferrell cell** (named after American meteorologist William Ferrell) exists at mid-latitudes between the Hadley and polar cells. The Ferrell cell is driven by the movement of the Hadley and polar cells and by exchange of energy between tropical and polar air masses in a region known as the *polar front*.

These three atmospheric circulation cells establish the major climate zones on Earth. Between 30°N and S is the **tropical zone**, or simply the **tropics**. The **temperate zones** lie between 30° and 60°N and S, and the **polar zones** are above 60°N and S (see Figure 2.8).

Atmospheric circulation cells create surface wind patterns

We've seen how the differential heating of Earth leads to zones of high and low atmospheric pressure. These pressure differences are important in explaining the movement

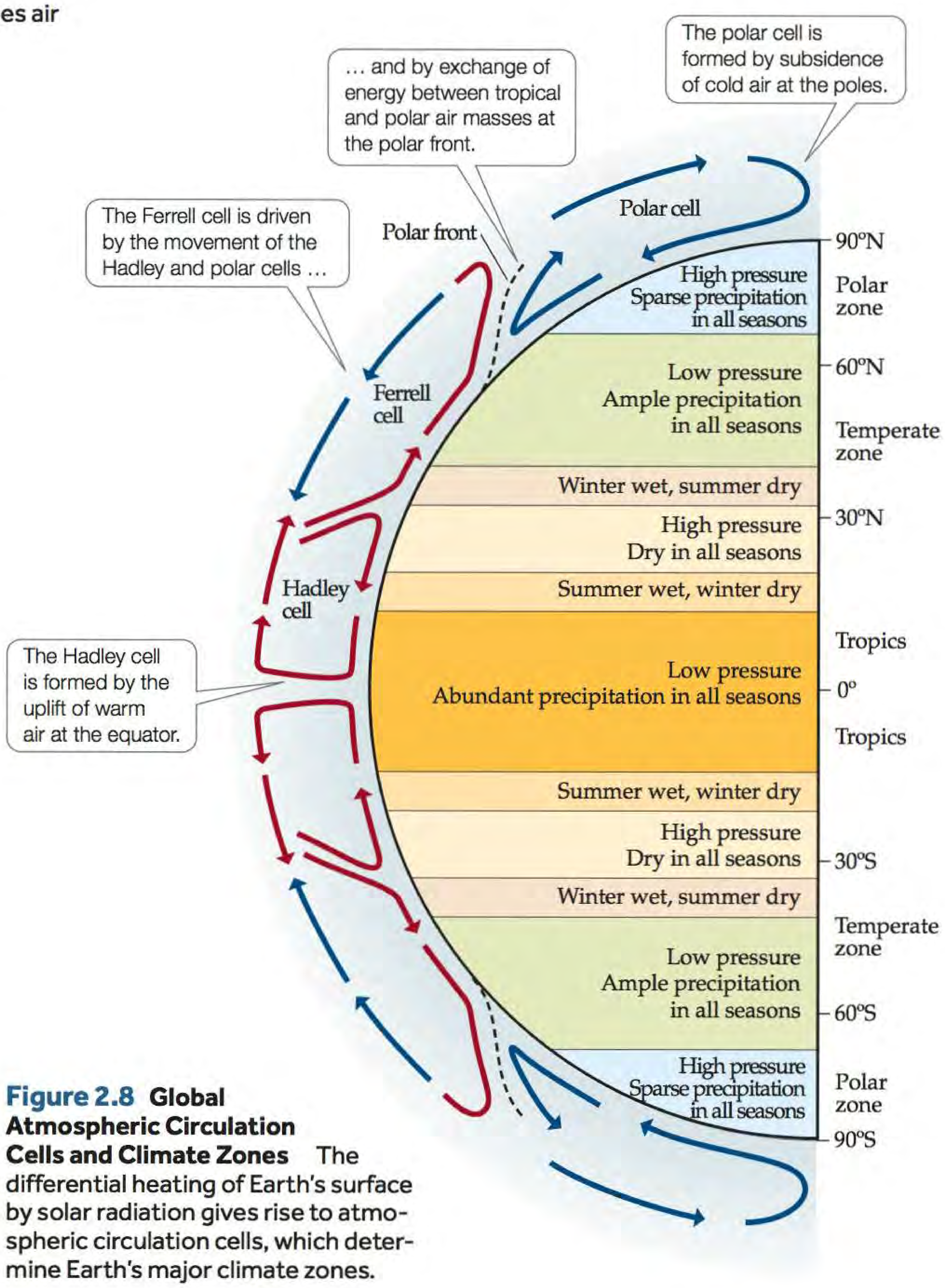
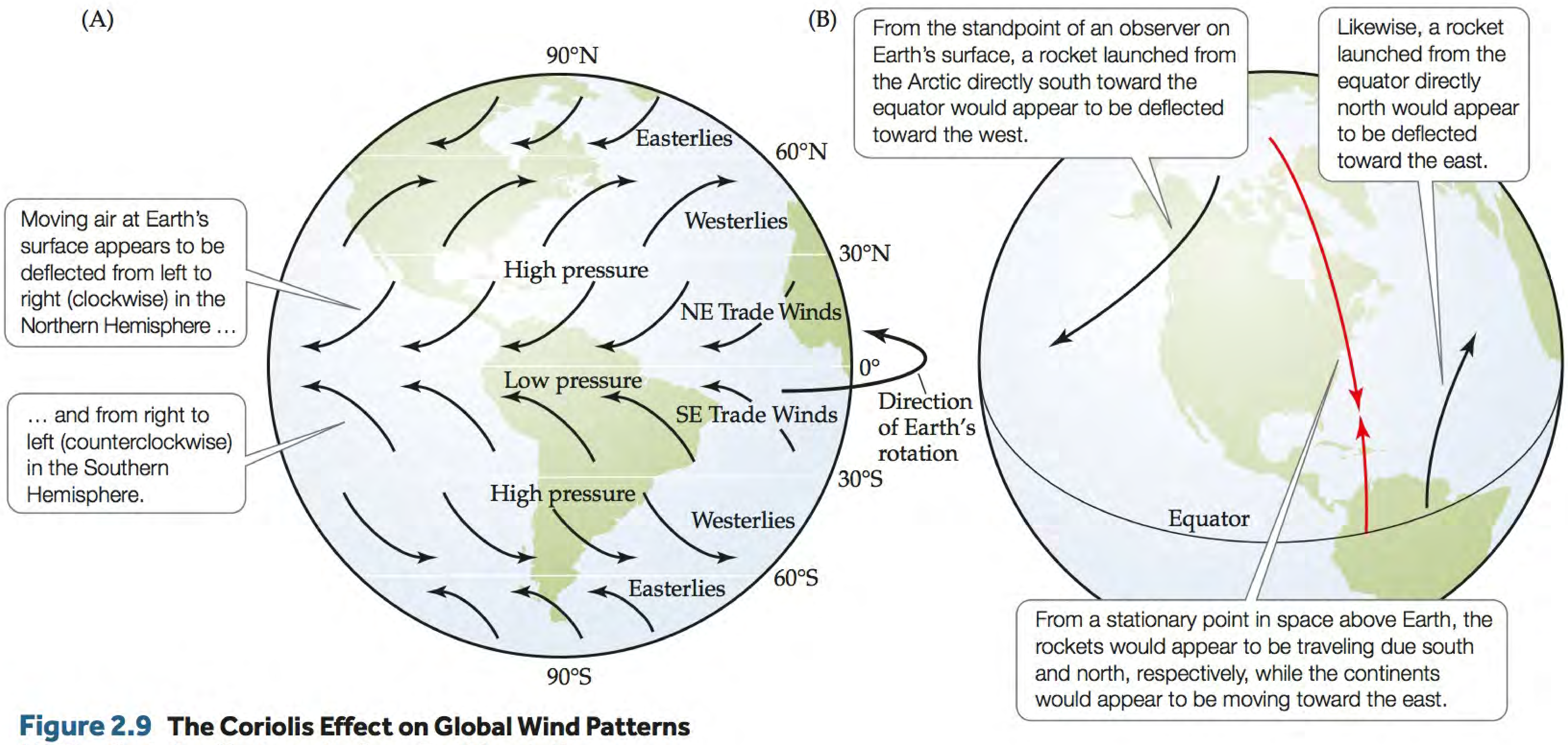


Figure 2.8 **Global Atmospheric Circulation Cells and Climate Zones** The differential heating of Earth's surface by solar radiation gives rise to atmospheric circulation cells, which determine Earth's major climate zones.



Moving air at Earth's surface appears to be deflected from left to right (clockwise) in the Northern Hemisphere …

… and from right to left (counterclockwise) in the Southern Hemisphere.

From the standpoint of an observer on Earth's surface, a rocket launched from the Arctic directly south toward the equator would appear to be deflected toward the west.

Likewise, a rocket launched from the equator directly north would appear to be deflected toward the east.

From a stationary point in space above Earth, the rockets would appear to be traveling due south and north, respectively, while the continents would appear to be moving toward the east.

Figure 2.9 The Coriolis Effect on Global Wind Patterns
(A) The Coriolis effect results from Earth's rotation.
(B) Visualization of the Coriolis effect using rockets.

of warm and cold air masses across Earth's surface. Winds flow from areas of high pressure to areas of low pressure. Thus, the areas of high and low pressure formed by atmospheric circulation cells give rise to consistent patterns of air movement at Earth's surface, known as *prevailing winds*. We might expect these winds to blow in straight lines from high- to low-pressure zones. However, from the standpoint of an observer on Earth, the prevailing winds appear to be deflected to the right (clockwise) in the Northern Hemisphere and to the left (counterclockwise) in the Southern Hemisphere (**Figure 2.9A**). The apparent deflection is associated with the rotation of Earth: to an observer on Earth's surface rotating around the planetary axis, the path of the wind appears curved (**Figure 2.9B**). This apparent deflection is known as the **Coriolis effect**. To an observer in a fixed position in outer space, however, there is no apparent deflection in the direction of the wind.

As a result of the Coriolis effect, surface winds blowing toward the equator from the high-pressure zones at 30°N and S are deflected to the west from the perspective of Earth's surface. These winds are known as the *trade winds* because of their importance to the global transport of trade goods in sailing ships during the fifteenth through the nineteenth centuries. Winds blowing toward the poles from those zones of high pressure, called *westerlies*, are deflected to the east. The presence of continental land masses interspersed with oceans complicates this idealized depiction of prevailing wind patterns (**Figure 2.10**).

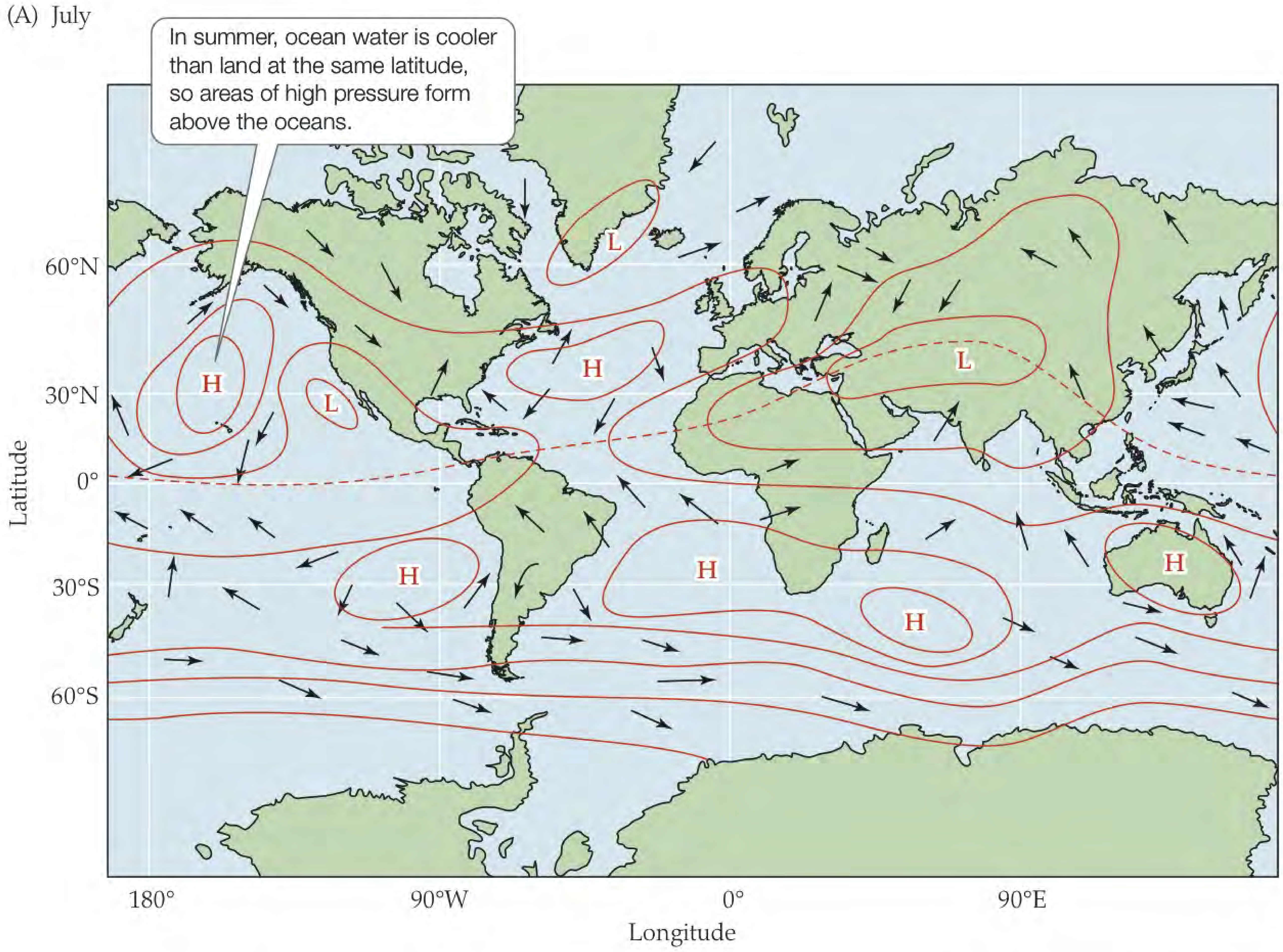
Water has a higher **heat capacity** than land, so it absorbs and stores more energy without its temperature changing than land does. For this reason, the land surface warms up more than ocean water in summer, but in winter the oceans retain more heat, and thus remain warmer, than land at the same latitude. As a result, seasonal air temperature changes are less extreme over the oceans than they are on land. In summer, air over the oceans is cooler and denser than that over land, and semipermanent zones of high pressure (*high-pressure cells*) form over the oceans, particularly around 30°N and S. In winter, the opposite situation exists: the air over the continents is cooler and denser than that over the oceans, so high-pressure cells develop in the temperate zones over large continental areas. Because winds blow from areas of high pressure to areas of low pressure, these seasonal shifts in pressure cells influence the direction of the prevailing winds. The effect of land areas on the development of these semipermanent pressure cells is more pronounced in the Northern Hemisphere than in the Southern Hemisphere because continental land masses make up a larger proportion of Earth's surface in the Northern Hemisphere.

Ocean currents are driven by surface winds

Wind moving across the ocean surface pushes the surface water. As a result of the Coriolis effect, the water appears to move at an angle to the wind. From the perspective of an observer on Earth, it is deflected to the right in the Northern Hemisphere and to the left in the Southern Hemisphere. For this reason, the pattern of ocean surface currents is similar to, but not identical to, the pattern of prevailing winds (**Figure 2.11**). The speed of ocean currents is usually only about 2%–3% of the wind speed. An average wind speed of 10 m per second (22 miles per

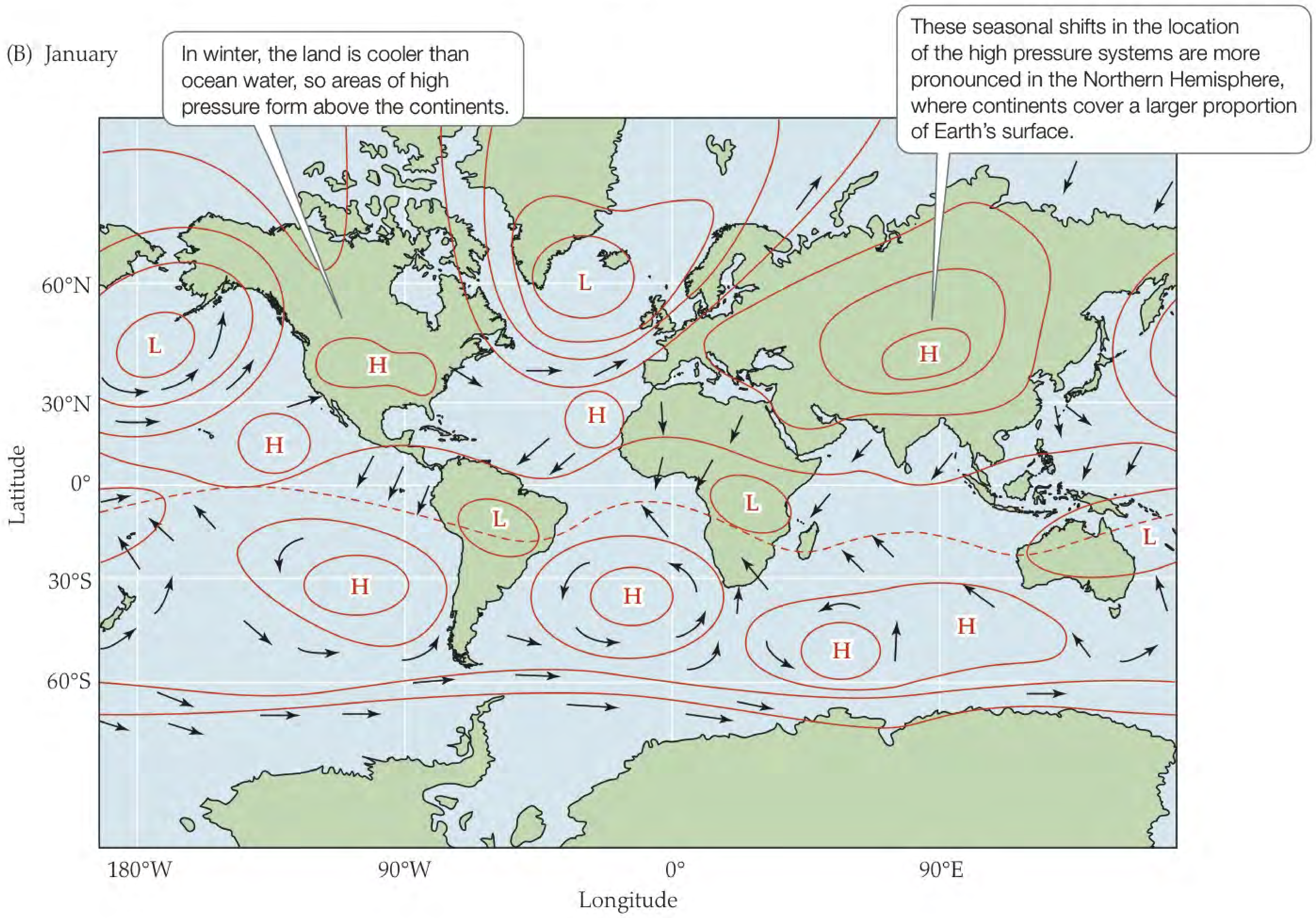
Figure 2.10 Prevailing Wind Patterns The difference in heat capacity between the oceans and the continents leads to seasonal changes in atmospheric pressure cells that influence prevailing wind patterns.

(A) July



In summer, ocean water is cooler than land at the same latitude, so areas of high pressure form above the oceans.

(B) January



In winter, the land is cooler than ocean water, so areas of high pressure form above the continents.

These seasonal shifts in the location of the high pressure systems are more pronounced in the Northern Hemisphere, where continents cover a larger proportion of Earth's surface.

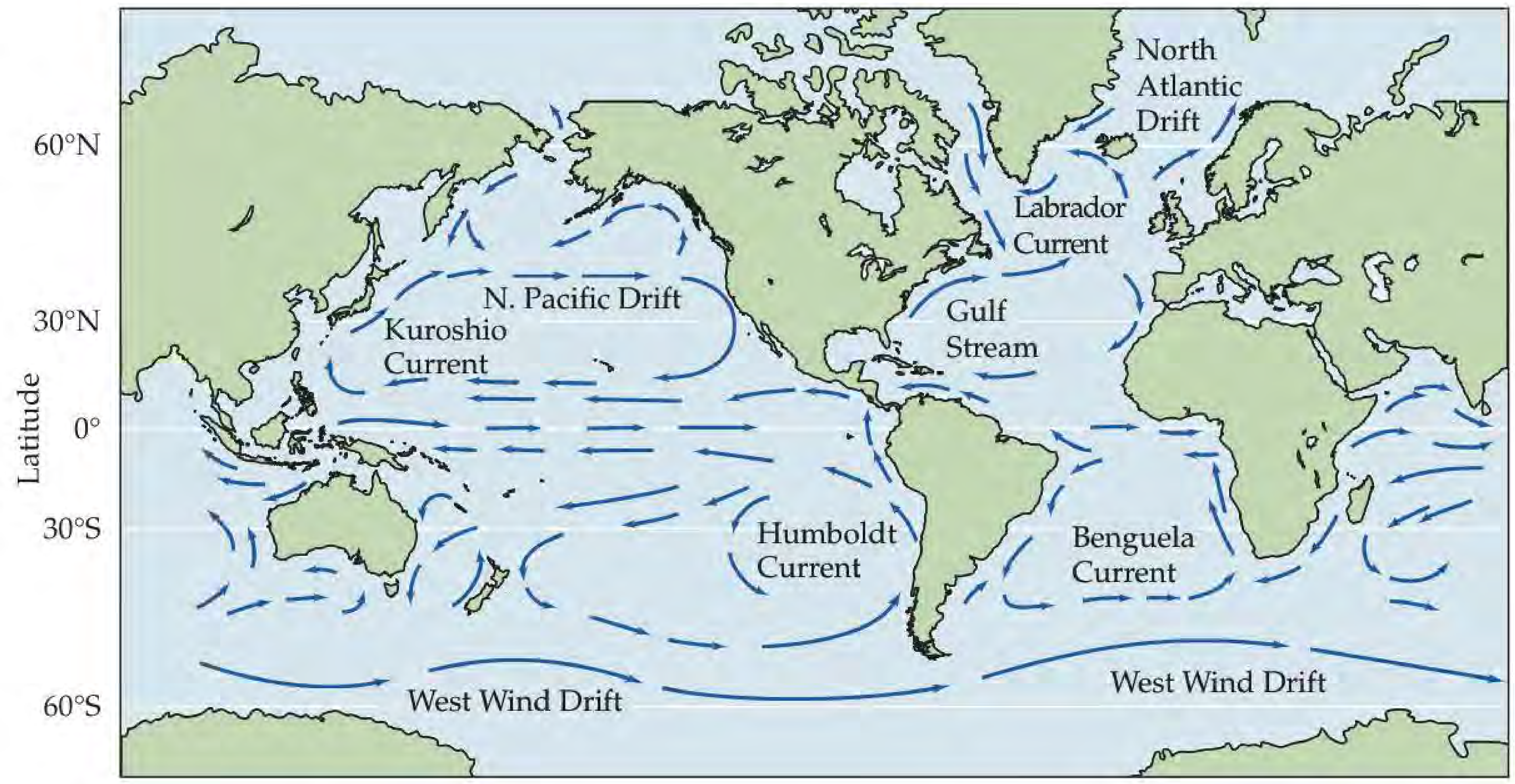


Figure 2.11 Global Ocean Surface Currents The major ocean surface currents are driven by the surface winds shown in Figure 2.10 but modified by the Coriolis effect.

hour) would therefore produce an ocean current moving at 30 cm per second (0.7 miles per hour). In the North Atlantic Ocean, current velocities may be as high as 200 cm per second (4.5 miles per hour).

Like air in the atmosphere, water in the ocean can move vertically as well as horizontally. Generally, the surface and deep layers of ocean water do not mix, because of differences in their temperature and salinity (concentration of dissolved salts). The surface waters—those above 75–200 m (250–600 feet)—are warmer and less saline, and therefore less dense, than the deeper, cooler ocean waters. When warm tropical surface currents reach polar regions, particularly the coasts of Antarctica and Greenland, their water loses heat to the surrounding environment and becomes cooler and denser. The water eventually cools enough for ice to form, which increases the salinity of the remaining unfrozen water. This combination of cooling and increasing salinity increases the density of the water, which sinks to deeper layers. The dense downwelling currents that result move toward the equator, carrying cold polar water toward the warmer tropical oceans.

These deep ocean currents connect with surface currents again at zones of **upwelling**, where deep ocean water rises to the surface. Upwelling occurs where prevailing winds blow nearly parallel to a coastline, such as off the western coasts of North and South America. The force of the wind, in combination with the Coriolis effect, causes surface waters to flow away from the coast (**Figure 2.12**),

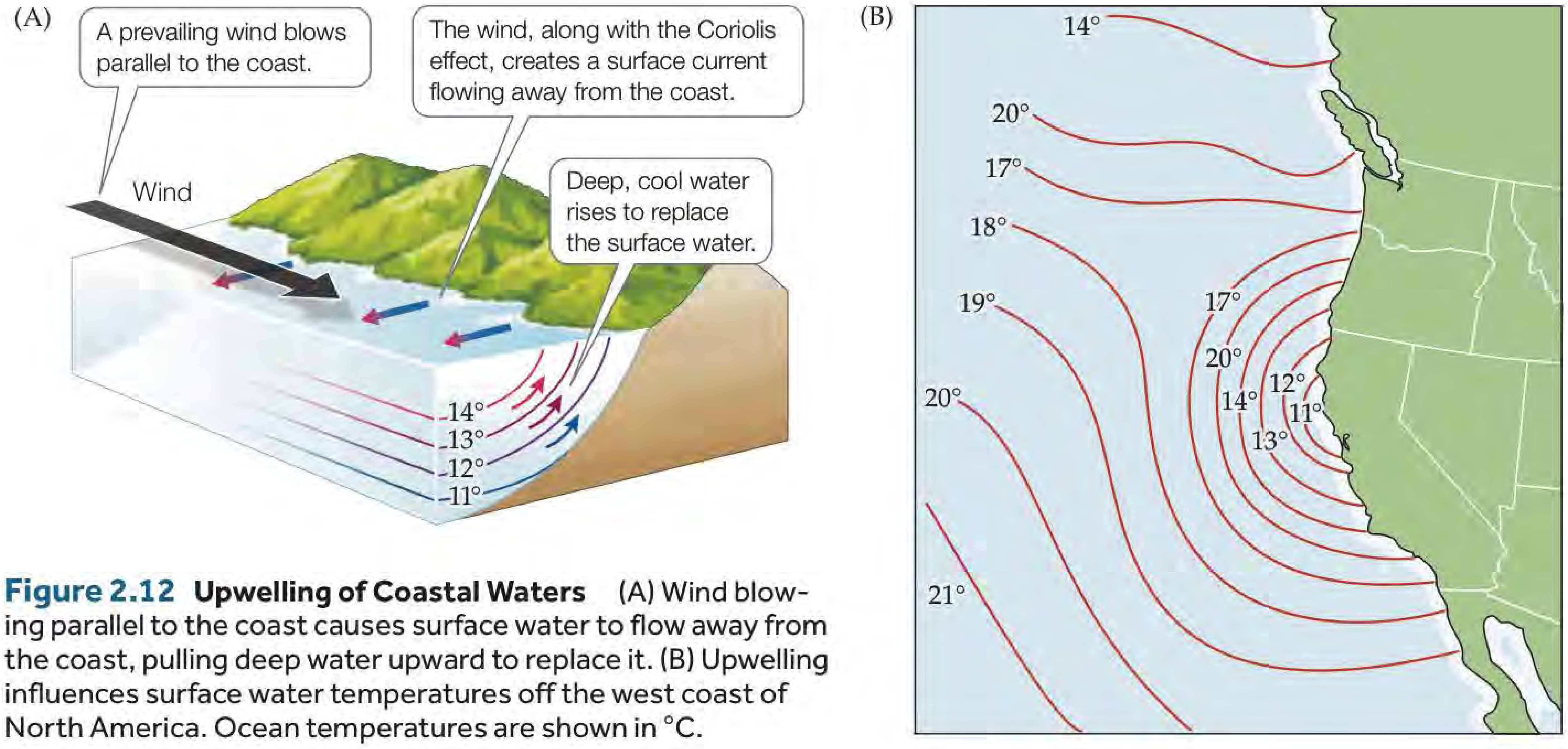


Figure 2.12 Upwelling of Coastal Waters (A) Wind blowing parallel to the coast causes surface water to flow away from the coast, pulling deep water upward to replace it. (B) Upwelling influences surface water temperatures off the west coast of North America. Ocean temperatures are shown in °C.

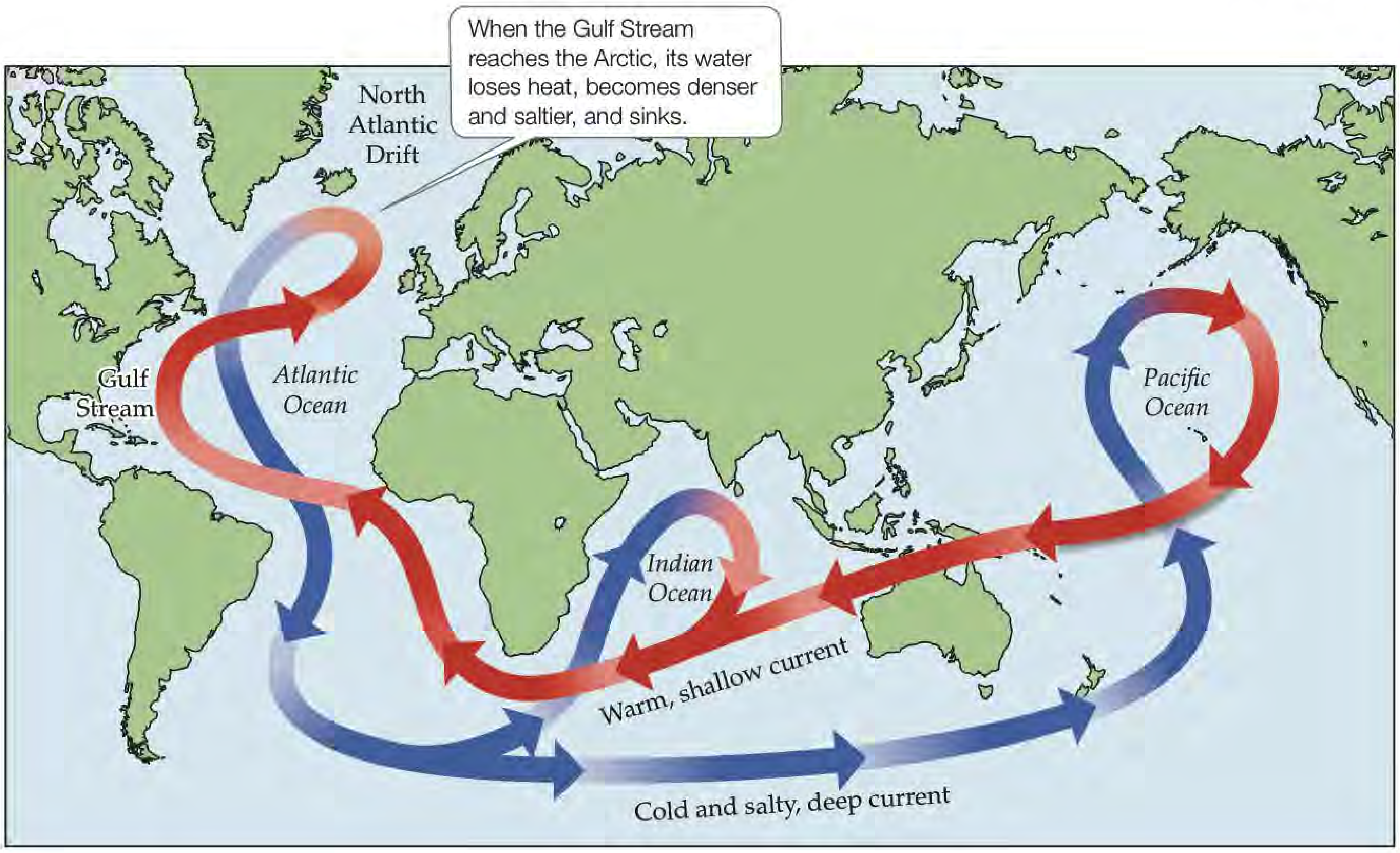


Figure 2.13 The Great Ocean Conveyor Belt An interconnected system of surface and deep ocean currents transfers energy between tropical and polar regions.

and deeper, colder waters rise to replace them. Upwelling also occurs in the westward-flowing equatorial Pacific Ocean. As a result of the Coriolis effect, water just to the north and south of the equator is deflected slightly away from the equator, causing divergence of surface water and a zone of upwelling.

Upwelling has important consequences for the local climate, creating a cooler, moister environment. Upwelling also has a strong effect on biological activity in the surface waters. When organisms in the surface waters die, their bodies—and the nutrients they contain—sink. Thus, nutrients tend to accumulate in deep water and in sediments at the ocean bottom. Upwelling brings these nutrients back to the *photic zone*, the layer of surface water where there is enough light to support photosynthesis. Upwelling zones are among the most productive open ocean ecosystems because these nutrients increase the growth of *phytoplankton* (small, free-floating algae and other photosynthetic organisms), which provide food for *zooplankton* (free-floating animals and protists), which in turn support the growth of their consumers.

Ocean currents influence the climates of the regions where they flow. For example, the Gulf Stream and North Atlantic Drift, a current system that flows from the tropical Atlantic northward to the North Atlantic (see Figure 2.11), contributes to warmer winters in Scandinavia than in locations at the same latitude in North America. In addition, winds blowing eastward across the Atlantic pick up heat from the ocean, which also contributes to a warmer climate in northern Europe. Winter temperatures on the west coast of Scandinavia are approximately 15°C (22°F) warmer than those on the coast of Labrador. This temperature difference is reflected in the vegetation: deciduous forests are common on the Scandinavian coast, while boreal forests of spruce and pine dominate the coast of Labrador. The Gulf Stream also keeps the North Atlantic ice-free most of the winter, whereas sea ice forms at the same latitude off the North American coast.

Ocean currents are responsible for about 40% of the heat exchanged between the tropics and the polar regions. Thus, ocean currents are sometimes referred to as the "heat pumps" or "thermal conveyers" of the planet. A large system of interconnected surface and deep ocean currents that links the Pacific, Indian, and Atlantic oceans, sometimes called the great ocean conveyor belt, is an important means of transferring heat to the polar regions (**Figure 2.13**).

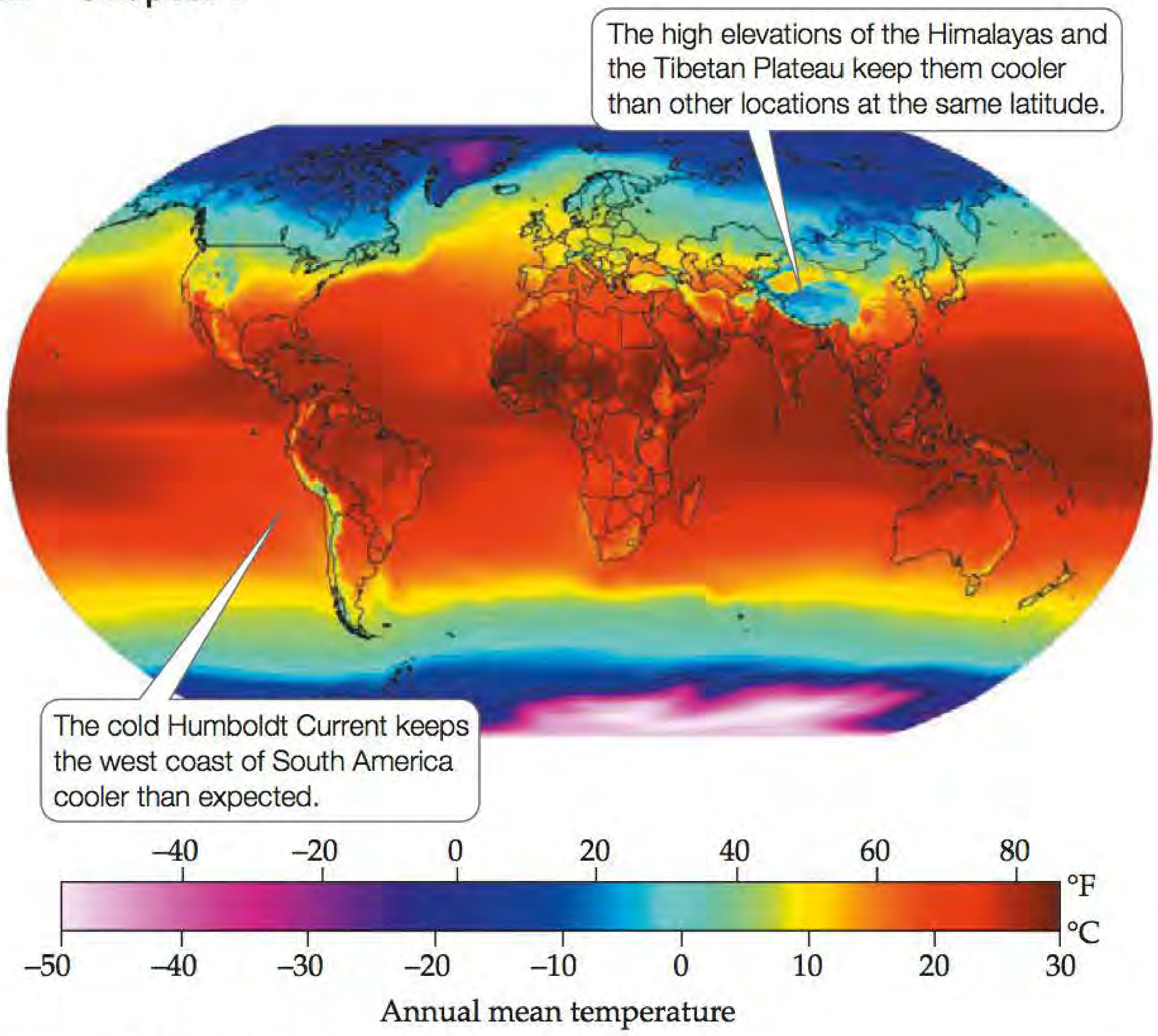
Now that we have seen how the differential heating of Earth's surface generates prevailing winds and ocean currents, let's examine the effects of these atmospheric and oceanic circulation patterns on Earth's climates, including global patterns of temperature and precipitation.

CONCEPT 2.3

Large-scale atmospheric and oceanic circulation patterns establish global patterns of temperature and precipitation.

Global Climate Patterns

Earth's climates reflect a variety of temperature and precipitation regimes, from the warm, wet climate of the tropics to the cold, dry climate of the Arctic and Antarctic. In this section, we examine these global patterns of temperature


The high elevations of the Himalayas and the Tibetan Plateau keep them cooler than other locations at the same latitude.

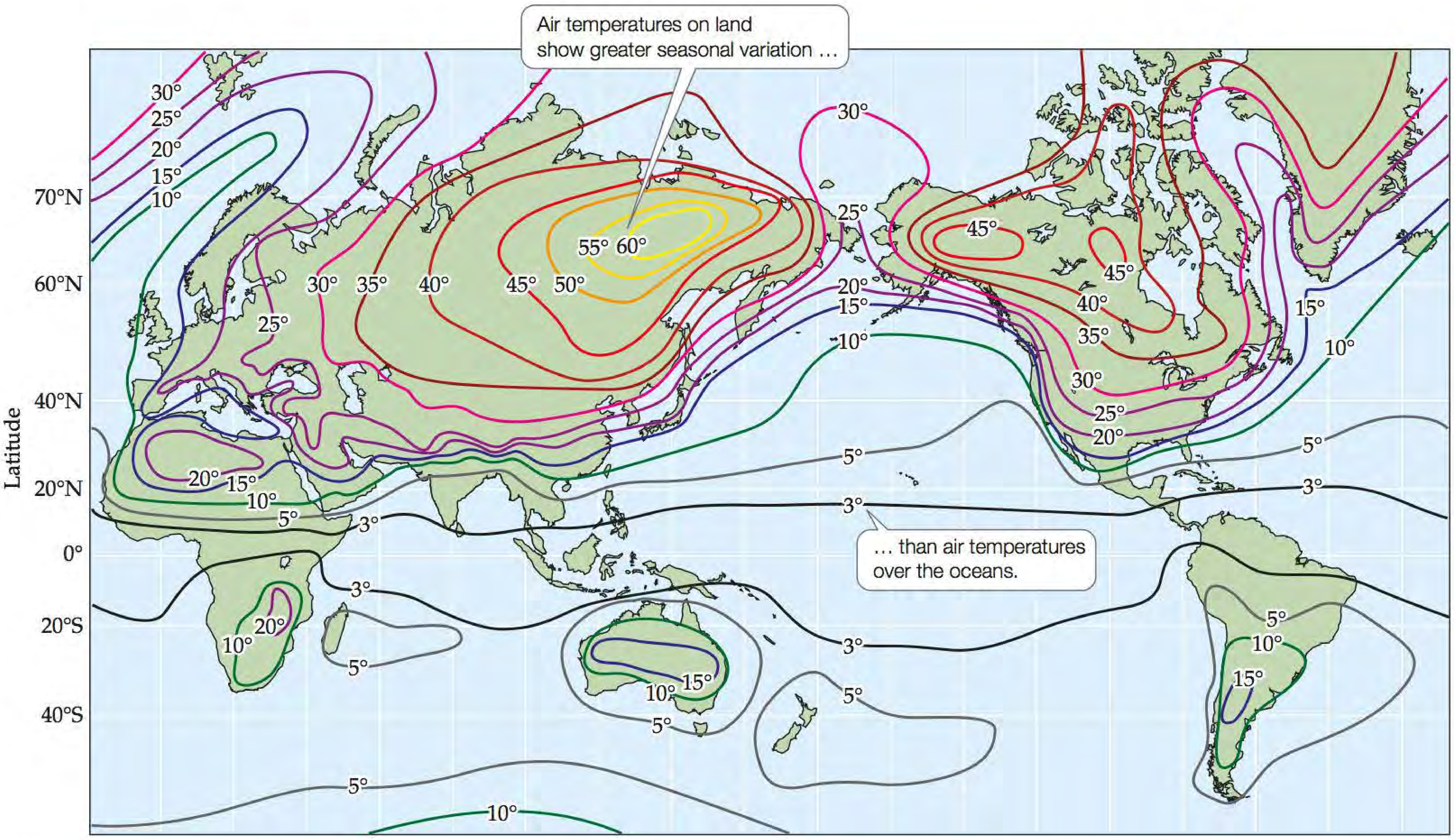
The cold Humboldt Current keeps the west coast of South America cooler than expected.

Figure 2.14 **Global Average Annual Temperatures** Average annual air temperatures tend to vary with latitude, but oceanic circulation and topography alter this pattern.

and precipitation and explore how both climate averages and climate variation are influenced by prevailing winds and ocean currents.

Oceanic circulation and the distribution and topography of continents influence global temperatures

The global pattern of solar radiation (see Figure 2.5) largely explains why temperatures at Earth's surface become progressively cooler from the equator to the poles (**Figure 2.14**). Note, however, that these changes in temperature are not exactly parallel with changes in latitude. Why do temperatures vary across the same latitude? Three major influences alter the global pattern of temperature: ocean currents, the distribution of land and water, and elevation. As we saw in the previous section, ocean currents contribute to a warmer climate in northern Europe than at North American locations of the same latitude. Similarly, the influence of the cold Humboldt Current is noticeable on the west coast of South America,


Air temperatures on land show greater seasonal variation …

… than air temperatures over the oceans.

Figure 2.15 **Annual Seasonal Temperature Variation** Seasonal temperature variation is expressed as the difference in average monthly temperature between the warmest and coldest months (in °C).

? What is the effect of continent size on the magnitude of seasonal temperature variation?

where temperatures are cooler than at similar latitudes elsewhere.

The difference in heat capacity between the oceans and the continents is not reflected in the average annual temperatures shown in Figure 2.14. Why is this so? Because the annual temperature *variation* is not depicted in that figure. Air temperatures over land show greater seasonal variation, with warmer temperatures in summer and colder temperatures in winter, than those over the oceans (**Figure 2.15**). This seasonal change has a major impact on the distribution of organisms, as we will see in later chapters.

Elevation above sea level has an important influence on continental temperatures. Note in Figure 2.14 the large difference in temperature between the Indian subcontinent and Asia. The sharp change in air temperature in this region is due to the influence of the Himalayas and the Tibetan Plateau. The change in elevation is extreme here, from about 150 m (500 feet) on the Ganges Plain in India to over 8,000 m (28,000 feet) in the highest peaks of the Himalayas in only 200 km (120 miles).

Why is it colder in mountains and highlands than in surrounding lowlands? Two factors contribute to the colder climates found at higher elevations. First, at higher elevations there are fewer air molecules to absorb the infrared energy radiating from Earth's surface. Thus, even though highlands may receive as much solar radiation as nearby lowlands, the heating of air by the ground surface is less effective because of the lower air density. Second, highlands exchange air more effectively with cooler air in the surrounding atmosphere. Because the atmosphere is warmed mainly by infrared radiation emitted by Earth's surface, the temperature of the atmosphere decreases with increasing distance from the ground. This decrease in temperature with increasing height above the surface is known as the **lapse rate**. In addition, wind velocity increases with increasing elevation because there is less friction with the ground surface. As a result, the decrease in air temperature with increasing elevation tends to follow the lapse rate.

Patterns of atmospheric pressure and topography influence precipitation

The locations of the Hadley, Ferrell, and polar circulation cells suggest that precipitation should be highest in the tropical latitudes between 23.5°N and S and in a band at about 60°N and S and should be lowest in zones around 30°N and S (see Figure 2.8). The African continent displays the pattern closest to this idealized precipitation distribution. However, there are substantial deviations from the expected latitudinal precipitation pattern in other areas, particularly in the Americas (**Figure 2.16**). These deviations are associated with the semipermanent

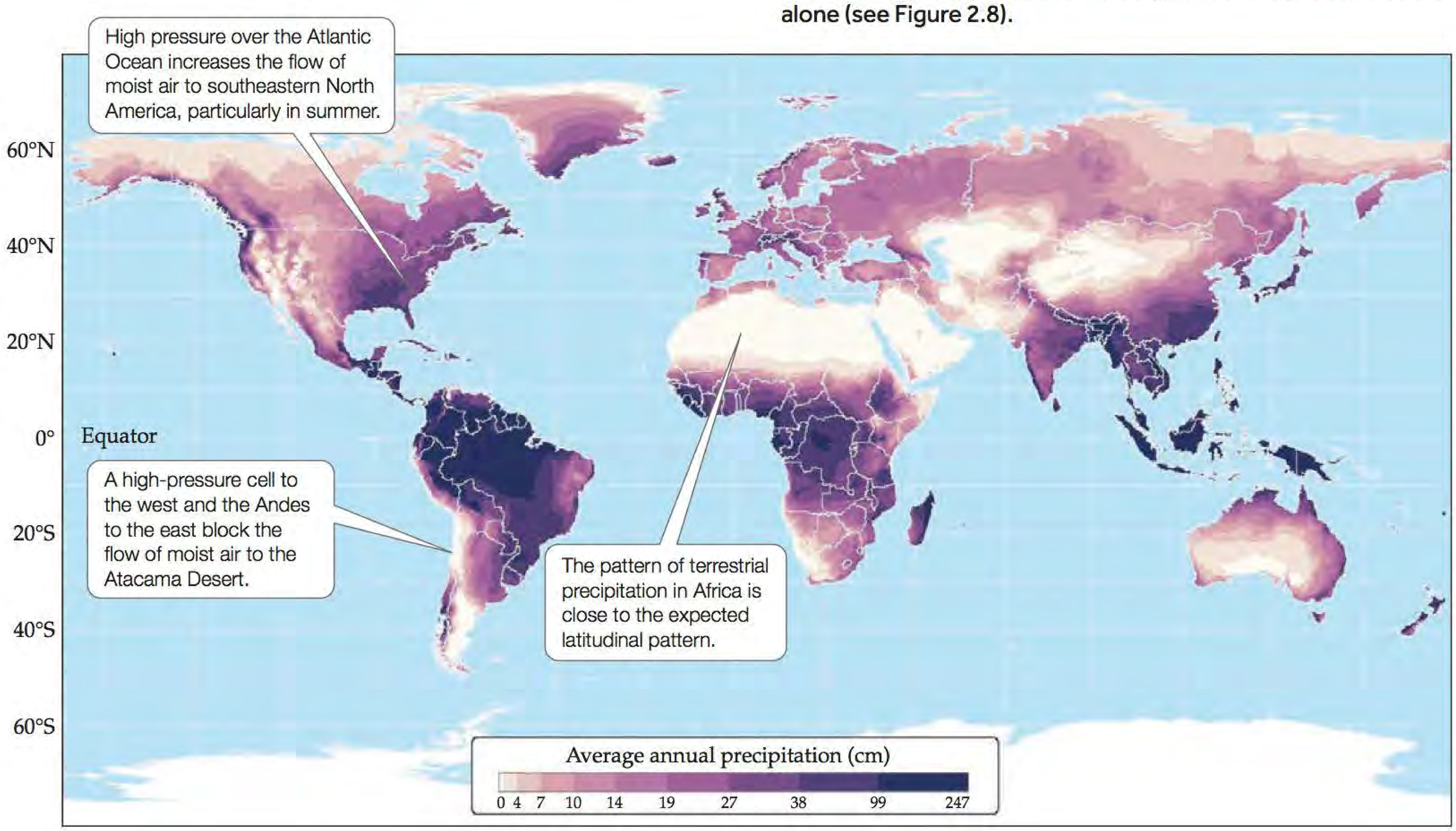


Figure 2.16 Average Annual Terrestrial Precipitation The latitudinal pattern of precipitation deviates from what would be expected based on atmospheric circulation patterns alone (see Figure 2.8).

High pressure over the Atlantic Ocean increases the flow of moist air to southeastern North America, particularly in summer.

A high-pressure cell to the west and the Andes to the east block the flow of moist air to the Atacama Desert.

The pattern of terrestrial precipitation in Africa is close to the expected latitudinal pattern.

high-pressure and low-pressure cells discussed earlier (see Figure 2.10) as well as with large mountain chains.

Pressure cells influence the movement of moist air from oceans to continents as well as cloud formation. For example, high pressure over the South Pacific Ocean decreases precipitation along the central west coast of South America. One of the driest deserts in the world, the Atacama, located along the Pacific coast of Chile, is associated with the presence of this high-pressure cell and with the blockage of air masses moving from the east by the Andes. In contrast, high pressure over the Atlantic Ocean increases the flow of moist air to southeastern North America, particularly in summer, increasing precipitation and supporting the occurrence of forests there.

Mountains also influence precipitation patterns by forcing air moving across them to rise, which enhances local precipitation. The effects of mountains, as well as those of oceans and vegetation, on regional climate patterns are addressed in the next section.

CONCEPT 2.4

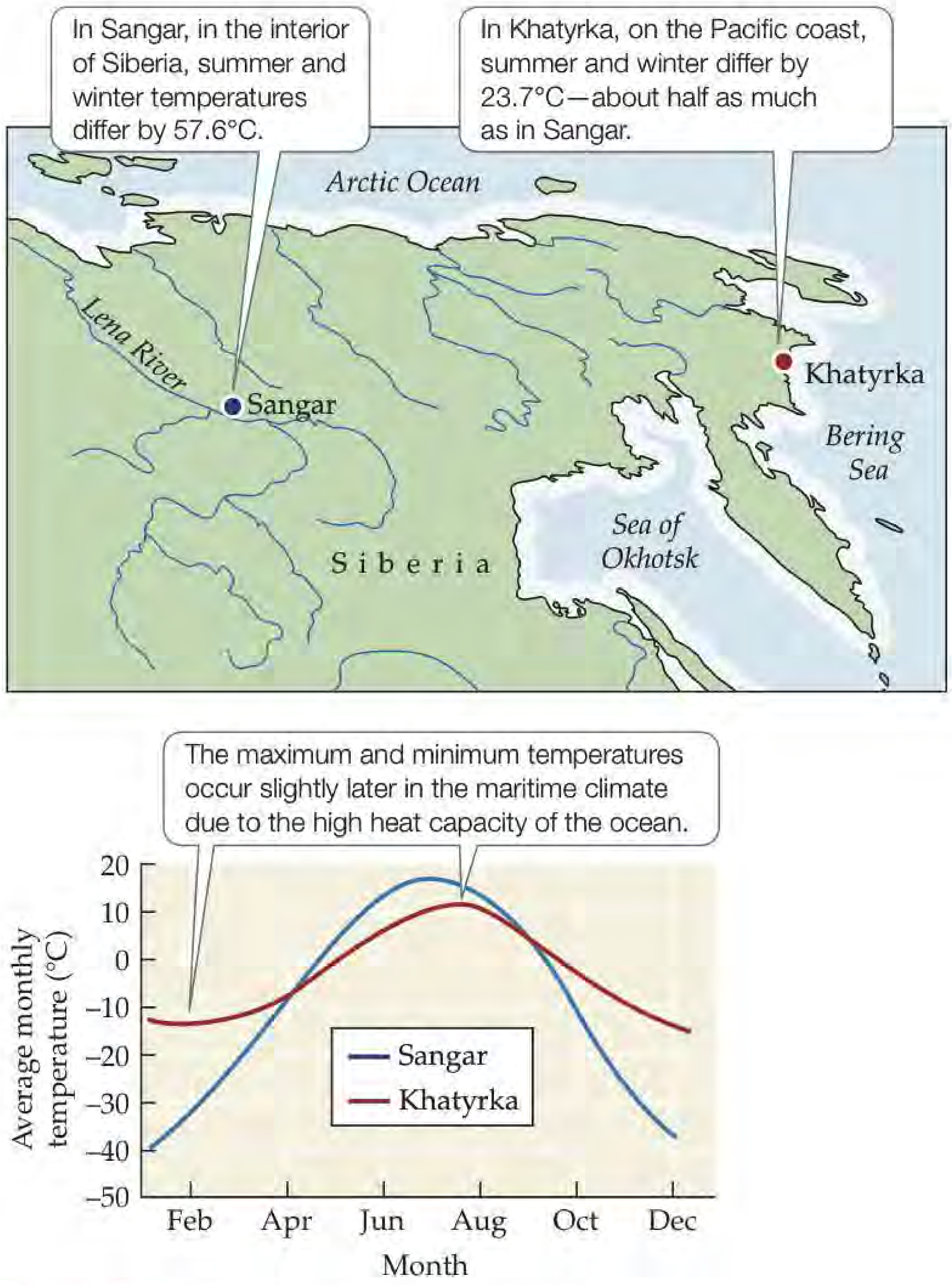
Regional climates reflect the influence of oceans and continents, mountains, and vegetation.

Regional Climate Influences

You may have noticed that as you travel from a coastal area to an inland location, the climate changes. This change in climate can be abrupt, particularly when you travel across a mountain chain. The daily variation in air temperature increases, humidity decreases, and precipitation decreases. These climate differences result from the effects of oceans and continents on regional energy balance and the influence of mountains on air flow and temperature. The vegetation often reflects these regional climate differences, exemplifying the effects of climate on the distributions of species and biological communities. The vegetation also has important effects on the climate through its influence on energy and water balance.

Proximity to oceans influences regional climates

Earlier we noted that water requires greater energy input to change its temperature (i.e., it has a higher heat capacity) than land. As a result, seasonal temperature changes are smaller over oceans than over continental areas (see Figure 2.15). In addition, oceans provide a source of moisture for cloud formation and precipitation. Coastal terrestrial regions that are influenced by an adjacent ocean have a **maritime climate**. Maritime climates are characterized by little variation in daily and seasonal temperatures, and they often have higher humidity than regions more distant from the coast. In contrast, areas centered in large continental land masses have a **continental climate**, which is characterized by much greater variation in daily and seasonal temperatures. Maritime climates occur in all climate zones, from tropical to polar. In the temperate zones, the influence of oceans on coastal climates tends to be accentuated on west coasts in the Northern Hemisphere and on east coasts in the Southern Hemisphere because of the prevailing wind patterns. Continental climates are limited to mid- and high latitudes (primarily in the temperate zones), where large seasonal changes in solar radiation accentuate the effect of the low heat capacity of land masses.


In Sangar, in the interior of Siberia, summer and winter temperatures differ by 57.6°C.

In Khatyrka, on the Pacific coast, summer and winter differ by 23.7°C—about half as much as in Sangar.

The maximum and minimum temperatures occur slightly later in the maritime climate due to the high heat capacity of the ocean.

Figure 2.17 Average Monthly Temperatures in a Continental and a Maritime Climate The difference in seasonal temperature variation between two locations in Siberia at about the same latitude and elevation illustrates the effect of the high heat capacity of ocean water.

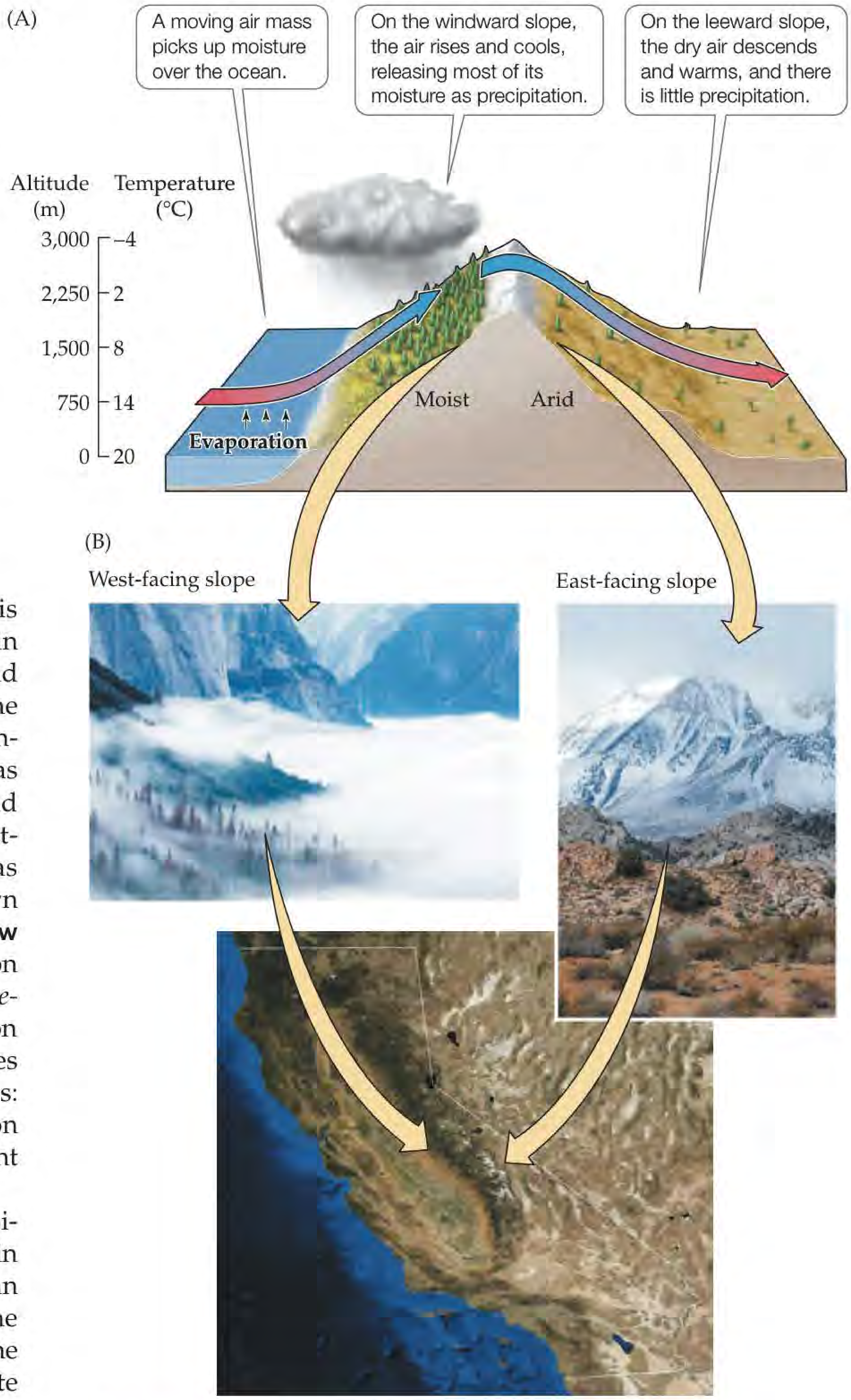
The influence of land and water on climate can be exemplified by comparing the seasonal temperature variation in locations at similar latitudes and elevations in Siberia (**Figure 2.17**). Sangar, a town on the Lena River in the middle of the Asian continent, exhibits more than double the seasonal temperature variation of Khatyrka, on the Pacific coast. Note that the maximum and minimum temperatures occur slightly later in the year in the maritime climate (Khatyrka), another reflection of the high heat capacity of the ocean and its effect on local climate.

Mountains influence wind patterns and gradients in temperature and precipitation

The effects of mountains on climate are visually apparent in the elevational patterns of vegetation, particularly in arid regions. As we move up a mountain, grasslands may abruptly change to forests, and at higher elevations, forests may give way to alpine grasslands. These abrupt shifts in vegetation patterns reflect the rapid changes in climate that occur over short distances in mountains as temperatures decrease, precipitation increases, and wind speed increases with elevation. What causes these abrupt changes? The climates of mountains are the product of the effects of topography and elevation on air temperatures, the behavior of air masses, and their own generation of unique local wind patterns.

Air moving across Earth's surface is forced upward when it encounters a mountain range. This uplifted air cools as it rises, and water vapor condenses to form clouds and precipitation. As a result, the amount of precipitation increases with elevation. This enhancement of precipitation in mountains is particularly apparent in north–south-trending mountain ranges on the slopes that face into the prevailing wind (the *windward* slopes). In the temperate zones, where the prevailing winds blow toward the east, moving air encounters the western slopes of mountain ranges (such as the Andes and the Sierra Nevada in the Americas) and loses most of its moisture as precipitation before cresting over the summits. The loss of moisture, as well as the warming of the air as it moves down the eastern slopes, dries the air mass (**Figure 2.18A**). This **rain-shadow effect** results in lower precipitation and soil moisture on the slopes facing away from the prevailing wind (the *leeward* slopes) and higher precipitation and soil moisture on the windward slopes. The rain-shadow effect influences the types and amounts of vegetation on mountain ranges: lush, productive plant communities tend to be found on the windward slopes, and sparser, more drought-resistant vegetation on the leeward slopes (**Figure 2.18B**).

Mountains can also generate local wind and precipitation patterns. Differences in the direction that mountain slopes face (referred to as the slope exposure or *aspect*) can cause differences in the amounts of solar radiation the slopes and surrounding flatlands receive. As we saw in the case of the large-scale circulation patterns that generate Hadley cells (see Figure 2.7), differences in solar heating of the ground surface can cause the uplift of air pockets that are warmer than the surrounding air. In the morning, east-facing slopes receive more solar radiation from the rising sun and thus become warmer than the surrounding slopes and lowlands. This differential heating creates localized upslope winds in the mountains. Depending on the moisture content of the air and the prevailing winds at higher elevations, clouds may form on the eastern flanks



A moving air mass picks up moisture over the ocean.

On the windward slope, the air rises and cools, releasing most of its moisture as precipitation.

On the leeward slope, the dry air descends and warms, and there is little precipitation.

Figure 2.18 The Rain-Shadow Effect (A) Precipitation tends to be greater on the windward slope of a mountain range than on the leeward slope. (B) Vegetation on west-facing and east-facing slopes in the Sierra Nevada of California reflects the rain-shadow effect.

? Which slope aspect (north, south, east, or west) on a north–south-trending mountain range in the tropical zone would have the highest precipitation, and which aspect would be in the rain shadow?

of the mountains. These clouds can generate local thunderstorms that may move off the mountains and into surrounding lowlands, increasing local precipitation.

At night, the ground surface cools, and the air above it becomes denser. Nighttime cooling is more pronounced at high elevations because the thinner atmosphere absorbs and reradiates less energy and allows more heat to be lost from the ground surface. Cold, dense air behaves like water, flowing downslope and pooling in low-lying areas. As a result, valley bottoms are the coldest sites in mountainous areas during clear, calm nights. This *cold air drainage* influences vegetation distributions in the temperate zones because of the higher frequency of subfreezing temperatures in low-lying areas. Daily upslope and nightly downslope winds are a common feature of many mountainous areas, particularly in summer when the input of solar radiation is highest.

At continental scales, mountains influence the movement, position, and behavior of air masses, and as a result, they influence temperature patterns in surrounding lowlands. Large mountain chains, or *cordilleras*, can act to channel the movement of air masses. The Rocky Mountains, for example, steer cold Arctic air through the central part of North America to their east and inhibit its movement through the intermountain basins to their west.

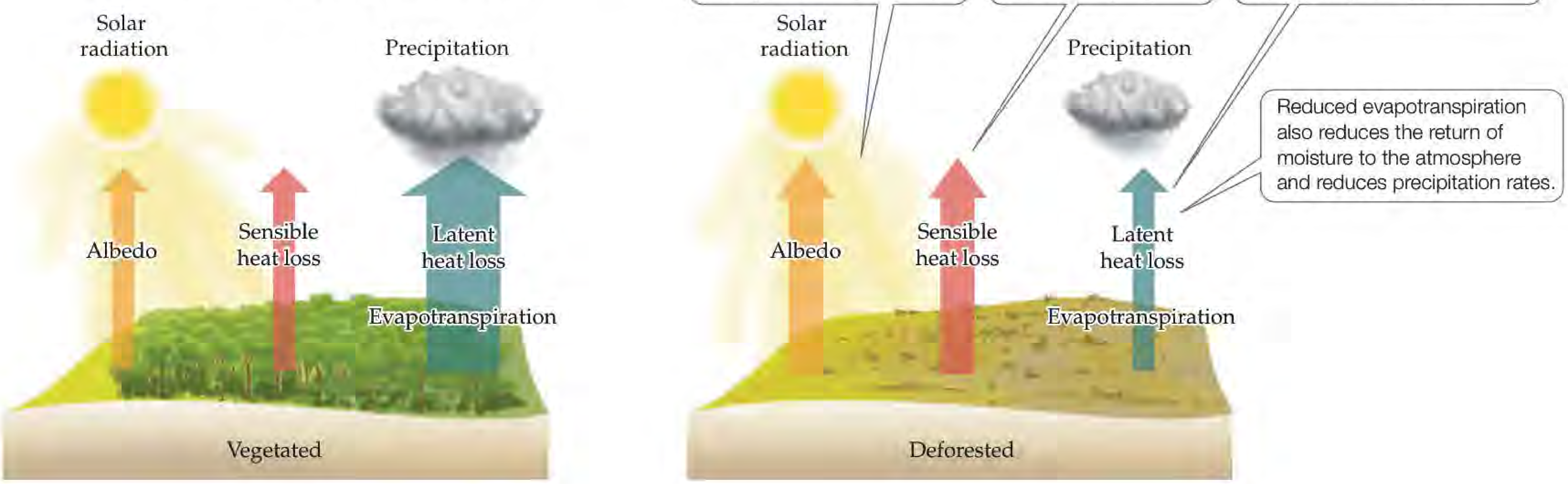
Vegetation affects climate via surface energy exchange

Climate determines where and how organisms can live, but organisms, in turn, influence the climate system in several ways. First, the amount and type of vegetation influences how the ground surface interacts with solar radiation and wind and how much water it loses to the atmosphere. The amount of solar radiation that a surface reflects, known as its **albedo**, is influenced by the presence and type of vegetation as well as by soil and topography. A coniferous forest, for example, is darker in color, and thus has a lower albedo, than most types of bare soil or grasslands, so the forest absorbs more solar energy.

The texture of Earth's surface is also influenced by vegetation. A rough surface, such as a savanna of mixed trees and grasses, allows greater transfer of energy to the atmosphere by wind (convection) than a smooth surface such as a grassland. This is because the vegetation disrupts air flow at the ground surface, causing turbulence that brings more surface air into the atmosphere. Finally, vegetation can cool the atmosphere through *transpiration* (evaporation of water from inside a plant via its leaves). The amount of transpiration increases with the amount of leaf area per unit of ground surface area. The sum of water loss by transpiration and by evaporation is referred to as **evapotranspiration**. Evapotranspiration transfers energy (latent heat) as well as water into the atmosphere, thereby reducing air temperature and soil moisture.

What happens to climate when the type or amount of vegetation is altered? This question is particularly important because of the current high rates of deforestation in the tropics: since 1990 about 129 million hectares (500,000 square miles) of tropical forest have been cut (FAO 2015). Loss of the trees increases the albedo of the land surface as bare soil is exposed and the trees are partially replaced with lighter-colored grasses (**Figure 2.19**). The higher albedo decreases the absorption of solar radiation, resulting in less heating of the land surface. However, the lower heat gain from solar radiation is more than offset by lower evapotranspirative cooling

Figure 2.19 The Effects of Deforestation Illustrate the Influence of Vegetation on Climate The conversion of forest to pasture in the tropics results in a number of changes in energy exchange with the atmosphere. (After Foley et al. 2003.)



Removing trees increases the albedo of the land surface, lowering its absorption of solar radiation.

The change in surface roughness increases sensible heat loss by convection (wind).

These cooling effects are more than offset by the warming effects of decreased latent heat loss by evapotranspiration.

Reduced evapotranspiration also reduces the return of moisture to the atmosphere and reduces precipitation rates.

(lower latent heat flux) due to loss of leaf area (Foley et al. 2003). Lower evapotranspiration rates not only reduce surface cooling, but also lead to lower precipitation because less moisture is returned from the ground surface to the atmosphere. Thus, the outcome of tropical deforestation may be a warmer, drier regional climate. Widespread deforestation may lead to climate change that is significant enough to inhibit reforestation and may thus lead to long-term changes in tropical ecosystems. The conversion of natural grasslands to crop production—a widespread human practice—can also affect climate, as you can evaluate in **Analyzing Data 2.1**.

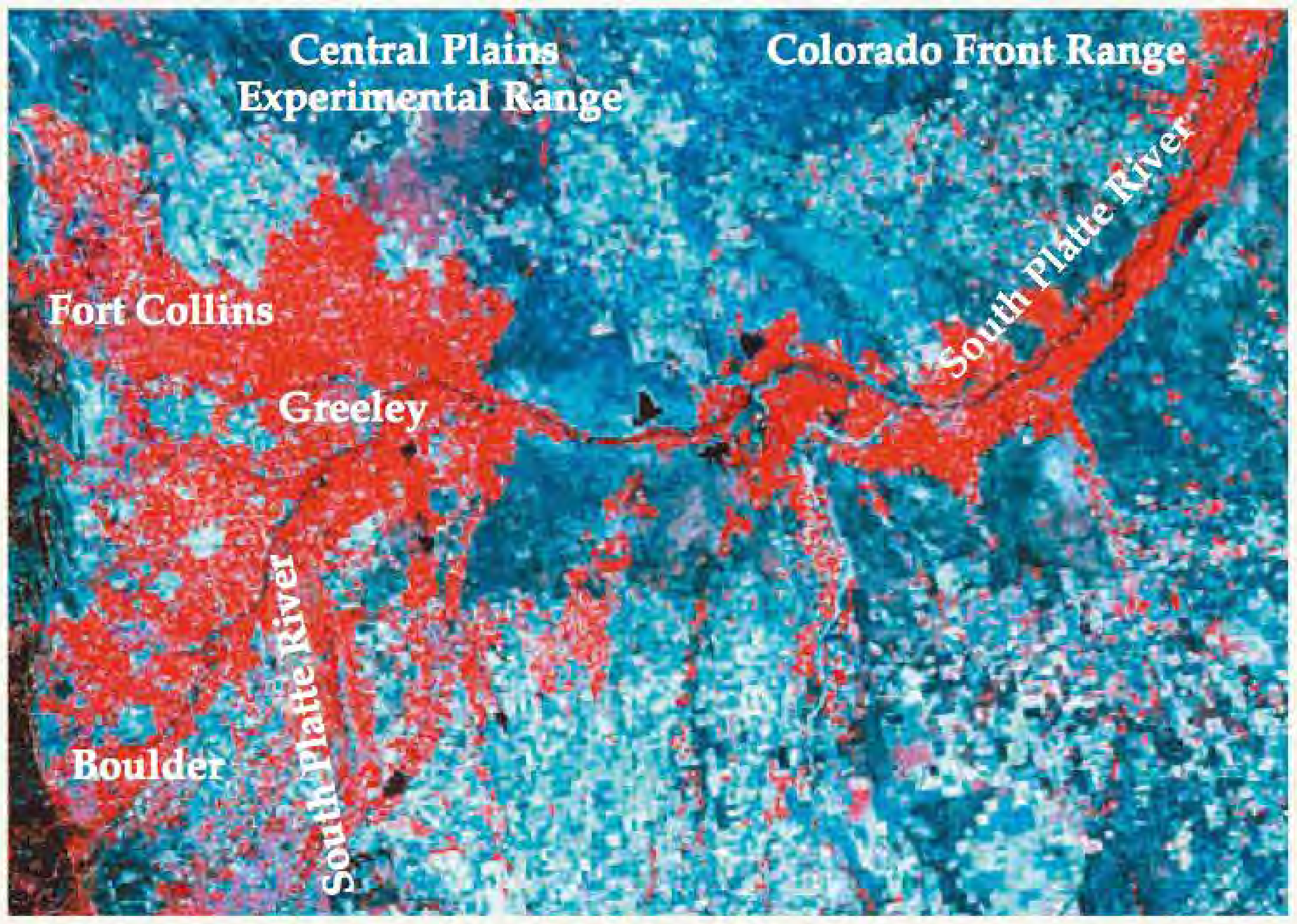
In Chapter 25 we will return to the effects of human activities on climate, especially over the past two centuries. Human activities, however, are not the only cause of long-term climate change. We turn next to the natural climate variation that has occurred throughout Earth's history.

ANALYZING DATA 2.1 How Do Changes in Vegetation Cover Influence Climate?

We've learned that the type and amount of vegetation can influence energy exchange at Earth's surface. As a result, human alteration of the land surface, such as tropical deforestation, can lead to changes in regional climate. Determining whether temperatures are likely to get warmer or cooler after such an alteration requires knowledge of the magnitude and direction of the changes in energy balance components.

For example, what happens when humans replace short-grass steppe, a type of grassland characteristic of the western Great Plains of the United States, with croplands? This vegetation change occurred along the South Platte River of northeastern Colorado in the latter part of the twentieth century, and its effects were evaluated by Chase and colleagues (1999).* Some of their data are presented here in the form of questions for your evaluation.

1. First consider changes in albedo. When sparse stands of light-colored grass (albedo = 0.26, meaning that 26% of incoming solar radiation is reflected) are replaced by dark green irrigated crops (albedo = 0.18), how does this influence absorption of solar radiation? If the incoming solar radiation is 470 watts per square meter (W/m^2), what is the difference in energy gain due to solar radiation as a result of the vegetation change? Would this change in albedo alone cause warming or cooling?
2. Next consider heat exchange due to sensible heat flux, including convection, which is related to the roughness of the surface. A dryland (nonirrigated) crop has approximately three times greater surface roughness than short-grass steppe. Which surface would have greater heat loss due to convection, assuming that surface temperatures are warmer than the atmosphere: a cropland or short-grass steppe? The estimated difference in heat exchange due to sensible heat flux associated with the land use change to a *dryland* crop is about 40 W/m^2. Would a combination of change in albedo (Question 1) and in surface roughness cause cooling, no net change, or warming?



Infrared Satellite Image of the South Platte River Drainage Basin, Colorado The Rocky Mountains are to the west. Red areas are irrigated cropland, and gray and dark blue areas are a mix of dryland crops and short-grass steppe.

3. Replacing short-grass steppe with *irrigated* crops, which have a higher leaf area per area of ground surface and higher soil moisture, alters the amount of energy lost via evapotranspiration (latent heat flux). Would this change result in more or less heat loss to the atmosphere relative to the short-grass steppe?
4. Taking both sensible and latent heat flux into account, the combined estimated difference in heat exchange associated with the land use change to irrigated cropland is about 60 W/m^2. Including the change in albedo from Question 1, would an irrigated crop surface have cooler or warmer temperatures relative to short-grass steppe?

See the companion website for a similar ANALYZING DATA exercise.

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*Chase, T. N., R. Pielke, Sr., T. G. F. Kittel, J. S. Baron and T. J. Stohlgren. 1999. Impacts on Colorado Rocky Mountain weather due to land use changes on the adjacent Great Plains. *Journal of Geophysical Research-Atmospheres* 104: 16673–16690

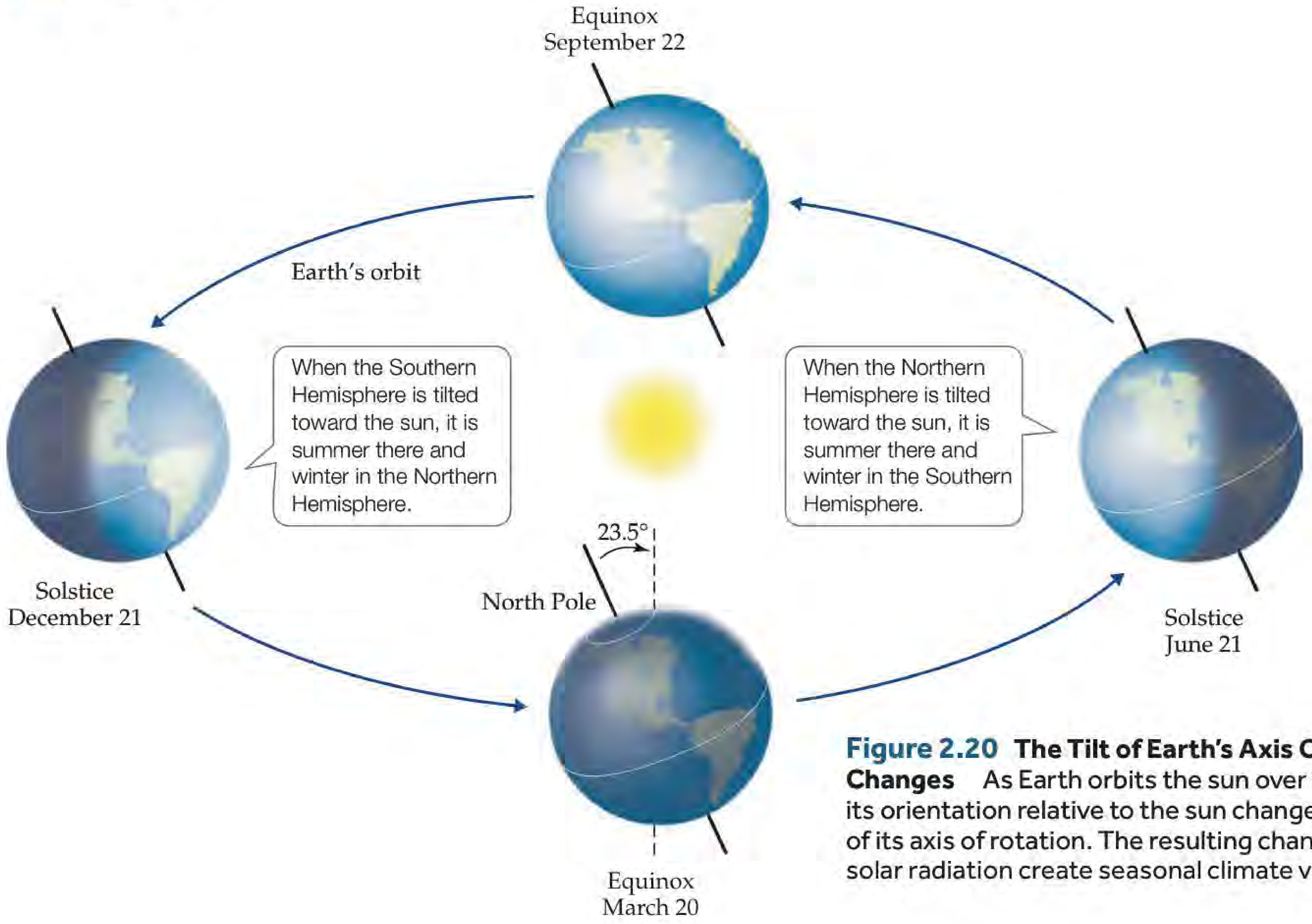


Figure 2.20 The Tilt of Earth's Axis Causes Seasonal Changes As Earth orbits the sun over the course of a year, its orientation relative to the sun changes because of the tilt of its axis of rotation. The resulting changes in the intensity of solar radiation create seasonal climate variation.

CONCEPT 2.5

Seasonal and long-term climate variation are associated with changes in Earth's position relative to the sun.

Climate Variation over Time

As noted at the beginning of this chapter, understanding climate variation is critical to understanding ecological phenomena such as the distributions of organisms. Climate variation at daily to multi-decadal time scales determines the range of environmental conditions experienced by organisms as well as the availability of the resources and habitats they need to survive. Long-term climate variation over hundreds and thousands of years influences the evolutionary history of organisms and the development of ecosystems. As we will see, the global climate has changed substantially over the course of Earth's history. In this section, we will review climate variation, from seasonal to 100,000-year time scales.

Seasonality results from the tilt of Earth's axis

The amount of sunlight striking any point on Earth's surface varies as Earth makes its 365.25-day journey around the sun. Earth's axis is tilted at an angle of 23.5° relative to the sun's direct rays (**Figure 2.20**). Thus, the angle and intensity of the rays striking any point on Earth change as Earth orbits the sun. This influence of the tilt of Earth's axis overrides the variation associated with seasonal changes in the distance between Earth and the sun due to Earth's slightly elliptical orbit. Earth is closest to the sun in January (at a point called the *perihelion*: 147 million miles) and farthest away in July (at the *aphelion*: 152 million miles). As we will see later, however, the effect of Earth–sun distance on climate is important over much longer time scales.

The temperate and polar zones experience pronounced changes in temperature associated with variation in solar radiation over the year. Summer occurs in the Northern Hemisphere from June to September, when that hemisphere is tilted toward the sun; at the same time, the Southern Hemisphere is oriented away from the sun and experiences its winter. The difference in solar radiation, and thus the temperature variation, between summer and winter increases from the tropics toward the poles. The seasonal changes in the angle of the sun affect not only the intensity of solar radiation, but also the length of the day. Above 66.5°N and S, the sun does not set for several days, weeks, or even months in summer. During the winter at these same latitudes, the sun does not rise high enough to warm the surface. Because air temperatures regularly drop below freezing during winter in the temperate and polar zones, seasonality in these zones is an important determinant of biological activity and strongly influences the distributions of organisms.

Seasonal changes in solar radiation are relatively small in the tropics compared with those in the temperate and polar zones. As a result, seasonality in the tropics is marked primarily by changes in precipitation rather than by changes in temperature. These seasonal changes are associated with the movement of the zone of maximum air uplift and precipitation, known as the **Intertropical Convergence Zone**, or **ITCZ**. This zone of maximum uplift corresponds with the part of the tropics where the sun strikes Earth most directly. Thus, the ITCZ moves from 23.5°N in June to 23.5°S in December, bringing the wet season with it (**Figure 2.21**).

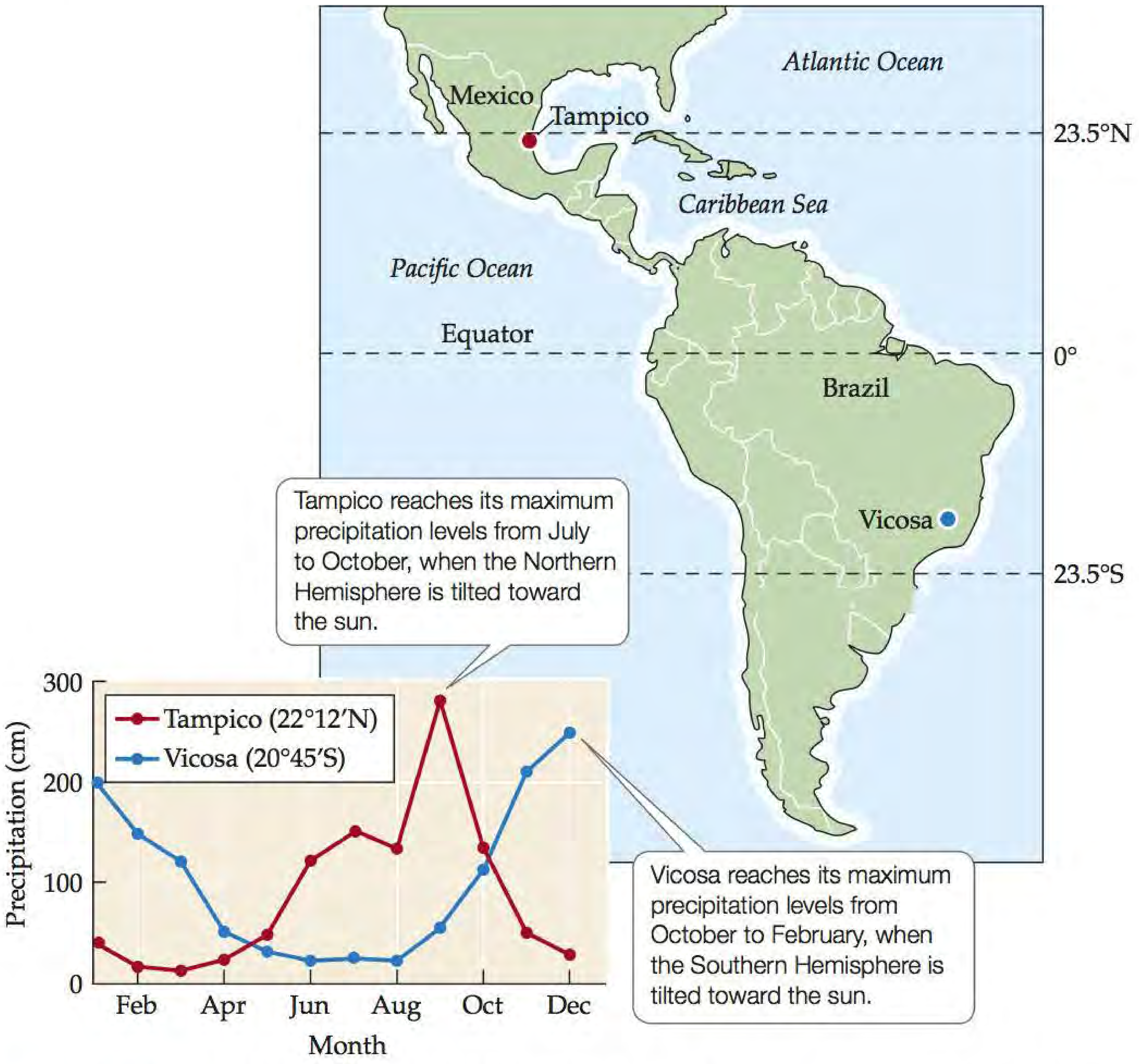
Seasonal changes in aquatic environments are associated with changes in water temperature and density

Aquatic environments in the temperate and polar zones also experience seasonal changes in temperature, but as we have seen, they are not as extreme as those on land. Liquid water becomes denser as it gets colder, and it has the unique property of being most dense at 4°C. Ice is less dense than liquid water and therefore forms on the surfaces of water bodies in winter. Because it has a higher albedo than open water, ice on the surface of lakes or polar oceans effectively prevents warming of the water below it.

Differences in water temperature (and thus water density) with depth result in the **stratification**, or layering, of water in oceans and lakes. Stratification has important implications for aquatic organisms because it determines the movement of nutrients and oxygen. Surface waters in lakes and oceans mix freely, but they are underlain by colder, denser layers of water that do not mix easily with the surface waters. In oceans, the surface waters mix with the subsurface layers only rarely—for example, in upwelling zones.

In temperate-zone lakes, seasonal changes in water temperature and density result in seasonal changes in stratification (**Figure 2.22**). In summer, the surface layer, or **epilimnion**, is the warmest and contains active populations of phytoplankton and zooplankton. The epilimnion is underlain by a zone of rapid temperature decline, called the **thermocline**. Below the thermocline is a stable layer of the densest, coldest water in the lake, known as the **hypolimnion**. In summer, dead organisms from the epilimnion will drop to the hypolimnion and bottom (*benthic*) zone, carrying nutrients and energy away from the surface layers.

During the fall, the air above the water surface cools, and the lake loses heat to the atmosphere. As the epilimnion cools, its density increases until it is the same as that of the layers below it. Eventually, the water at all depths of the lake has the same temperature and density, and winds blowing on the surface lead to a mixing of surface and deep layers, known as lake **turnover**. This mixing is important for recycling of the nutrients that are lost from the epilimnion during summer. In addition, lake turnover moves oxygen into the hypolimnion and the sediments at the lake bottom. The replenishment of nutrients at the surface and of oxygen at the bottom, where it is used up by the respiration of aerobic bacteria during summer, increases biological activity throughout the lake. Turnover occurs again in spring when the surface ice melts and the lake water has a uniform density once again.



Tampico reaches its maximum precipitation levels from July to October, when the Northern Hemisphere is tilted toward the sun.

Vicosa reaches its maximum precipitation levels from October to February, when the Southern Hemisphere is tilted toward the sun.

Figure 2.21 Wet and Dry Seasons and the ITCZ Seasonality of precipitation in the tropics is associated with movement of the Intertropical Convergence Zone (ITCZ) between the tropics of the Northern and Southern Hemispheres. Thus, Tampico, Mexico, reaches its maximum precipitation levels from July to October and has a dry season from November to April, whereas Viçosa, Brazil, has a wet season from October to February and a dry season from April to August.

Climate variation over years and decades results from changes in atmospheric pressure cells

Peruvian fisherman have long been aware of times when the normally

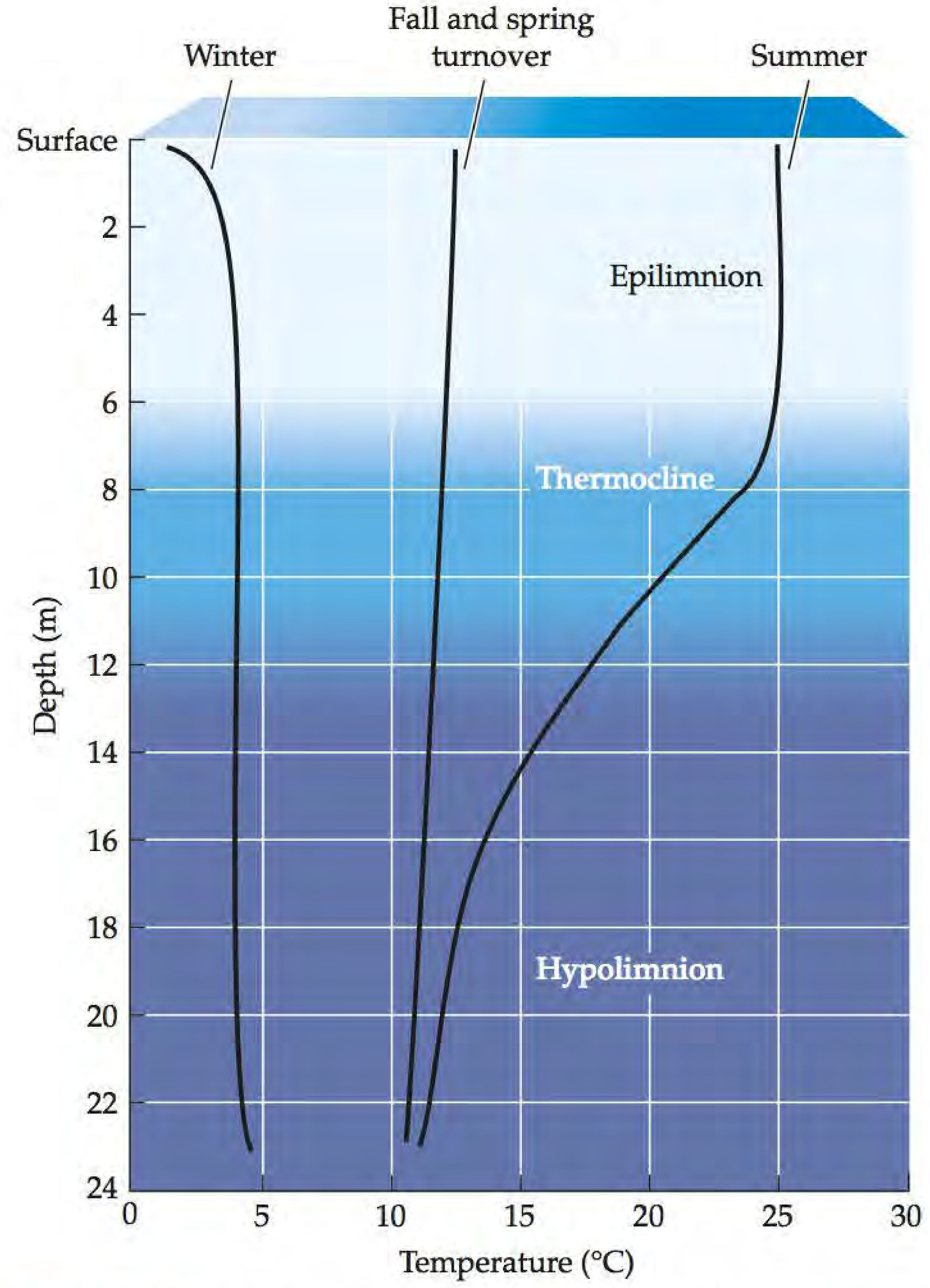


Figure 2.22 **Lake Stratification** Lake stratification, which occurs primarily in summer in temperate and polar regions, results from the effects of temperature on water density. Seasonal changes in water temperature result in the turnover of water that mixes little during summer and winter.

? Why would seasonal changes in lake stratification be unlikely to occur in tropical lakes?

Figure 2.23 **The El Niño Southern Oscillation (ENSO)** (A, B) Departures from long-term average ocean temperatures in equatorial waters of the Pacific under (A) El Niño conditions and (B) La Niña conditions. (C, D) El Niño events have widespread climate effects that vary seasonally, altering temperature and precipitation patterns at a global scale.

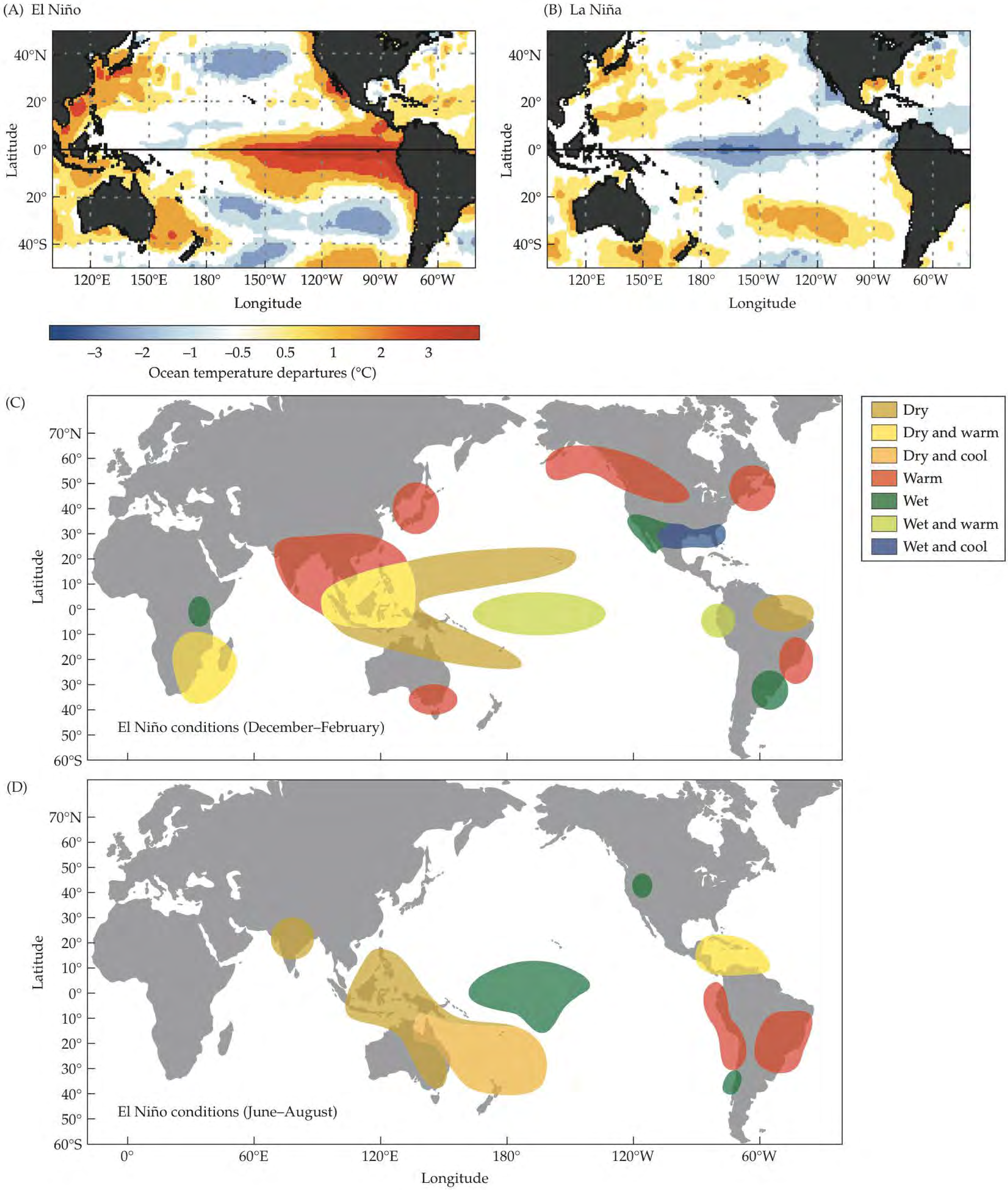
productive ocean waters hold few fish and the weather becomes extremely wet. They named these climate episodes El Niño, for the Christ child, because they usually started around Christmas. El Niño events are associated with a switch (or oscillation) in the positions of high-pressure and low-pressure cells over the equatorial Pacific, which leads to a weakening of the easterly trade winds that normally push warm water toward Southeast Asia. Climatologists refer to this oscillation and the climate changes associated with it as the **El Niño Southern Oscillation**, or **ENSO**. Its underlying causes are still not well understood. The frequency of ENSO is somewhat irregular, but it occurs at intervals of 3–8 years and generally lasts for about 18 months. During El Niño events, the upwelling of deep ocean water off the coast of South America ceases as the easterly winds weaken or, in some events, shift to westerly winds (**Figure 2.23A**). ENSO also includes La Niña events, which are stronger-than-average phases of the normal pattern, with high pressure off the coast of South America and low pressure in the western Pacific (**Figure 2.23B**). La Niña events usually follow El Niño events but tend to be less frequent.

ENSO is associated with unusual climate conditions, even at localities distant from the tropical Pacific, through its complex interactions with atmospheric circulation patterns (**Figure 2.23C,D**). El Niño events are associated with unusually dry conditions in the Malay Archipelago, other parts of Southeast Asia, and Australia. The likelihood of fires in the grasslands, shrublands, and forests of these areas increases as precipitation decreases and vegetation dries out. In contrast, in the southern United States and northern Mexico, El Niño events may increase precipitation, while the ensuing La Niña events bring drought conditions. The increased plant growth associated with an El Niño event, followed by dry La Niña conditions, intensifies fires in the southwestern United States (Veblen et al. 2000).

Similar atmospheric pressure–ocean current oscillations occur in the North Atlantic Ocean. The **North Atlantic Oscillation** affects climate variation in Europe, in northern Asia, and on the east coast of North America. Another long-term oscillation in sea surface temperature and atmospheric pressure, known as the **Pacific Decadal Oscillation**, or **PDO**, was described for the North Pacific after its influence on salmon numbers was discovered, as described in the Case Study earlier in this chapter. The PDO affects climate in ways similar to ENSO and can moderate or intensify the effects of ENSO. The effects of the PDO are felt primarily in northwestern North America, although southern parts of North America, Central America, Asia, and Australia may also be affected. The PDO and the North Atlantic Oscillation have been linked to long-term droughts in the United States (e.g., the U.S. Dust Bowl in the 1930s; see the Case Study for Chapter 25). We will return to the PDO in the Case Study Revisited.

Long-term climate change is associated with variation in Earth's orbital path

Antarctica today is almost completely covered with ice, and life is limited to its outer margins. Yet evidence from fossils indicates that there were once forests in interior parts of Antarctica and that dinosaurs once roamed the continent. Based on our knowledge of the biology of trees and dinosaurs, we can conclude that there must have been a warmer climate in the Antarctic past. What could have caused the climate to change so dramatically? The latitudinal position of Antarctica has shifted over


(A) El Niño
(B) La Niña
40°N
20°
0°
20°
40°S
Latitude
120°E
150°E
180°
150°W
120°W
90°W
60°W
Longitude
–3
–2
–1
–0.5
0.5
1
2
3
Ocean temperature departures (°C)
(C)
70°N
60°
50°
40°
30°
20°
10°
0°
10°
20°
30°
40°
50°
60°S
Latitude
El Niño conditions (December–February)
Dry
Dry and warm
Dry and cool
Warm
Wet
Wet and warm
Wet and cool
(D)
El Niño conditions (June–August)
0°
60°E
120°E
180°
120°W
60°W
Longitude

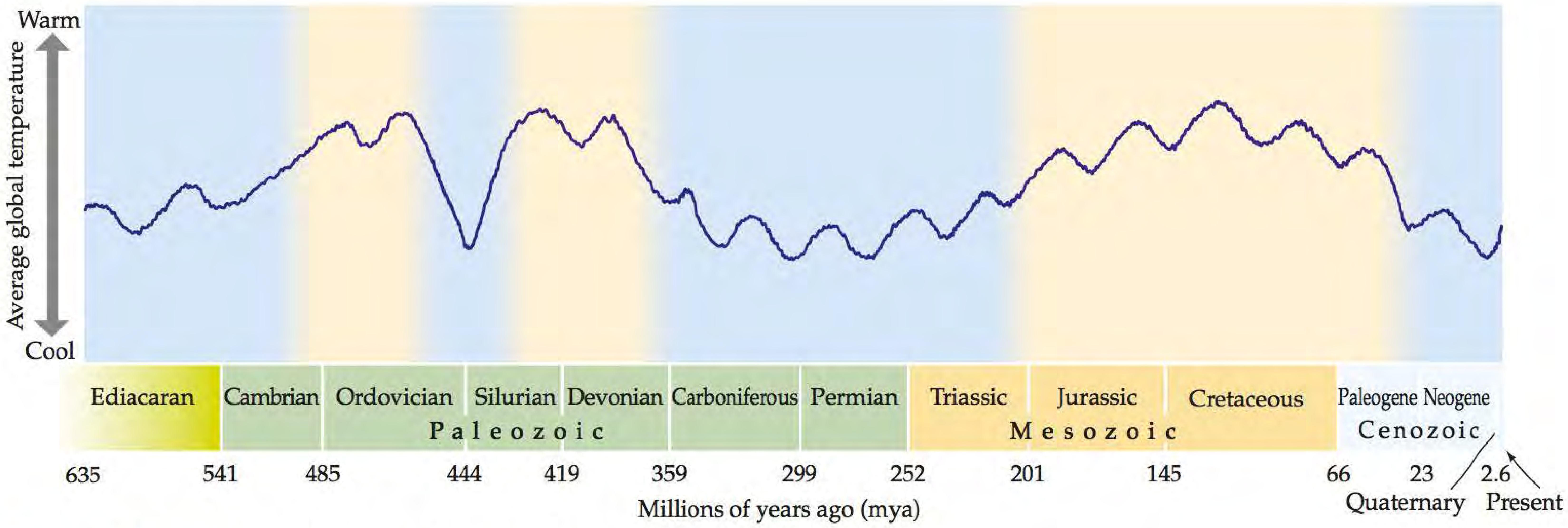


Figure 2.24 Long-Term Record of Average Global Temperature Global climate patterns have cycled between warm and cool periods for the past 500 million years.

hundreds of millions of years because of *continental drift*, the movement of land masses across the surface of Earth as they float on the mantle beneath the crust (described in Concept 18.2). Continental drift could have resulted in a warmer or cooler climate as Antarctica moved closer to or farther away from the equator. However, the age of many of the Antarctic fossils, along with a reconstruction of the movements of the continent, indicates that Antarctica was in a latitudinal position similar to today's when the forests and dinosaurs occurred there (190–65 million years ago). Thus, Earth's climate must have once been much warmer than it is now.

Many lines of evidence indicate that Earth has experienced several episodes of warmer and cooler climates over the past 500 million years (**Figure 2.24**). During the course of Earth's history, the amount of radiation emitted by the sun has been gradually increasing, so that factor does not explain these irregular cycles of long-term global climate change. Hypotheses for the causes of these climate shifts have focused on changes in the concentrations of greenhouse gases in the atmosphere. Warmer periods are associated with higher concentrations of greenhouse gases, while cooler periods are associated with lower concentrations of those gases.

Earth is currently in a cool climate phase that has lasted about 3 million years. This phase has been characterized by regular periods of cooling, accompanied by the formation and advance of glaciers, followed by periods of warming, accompanied by glacial melting. The peaks

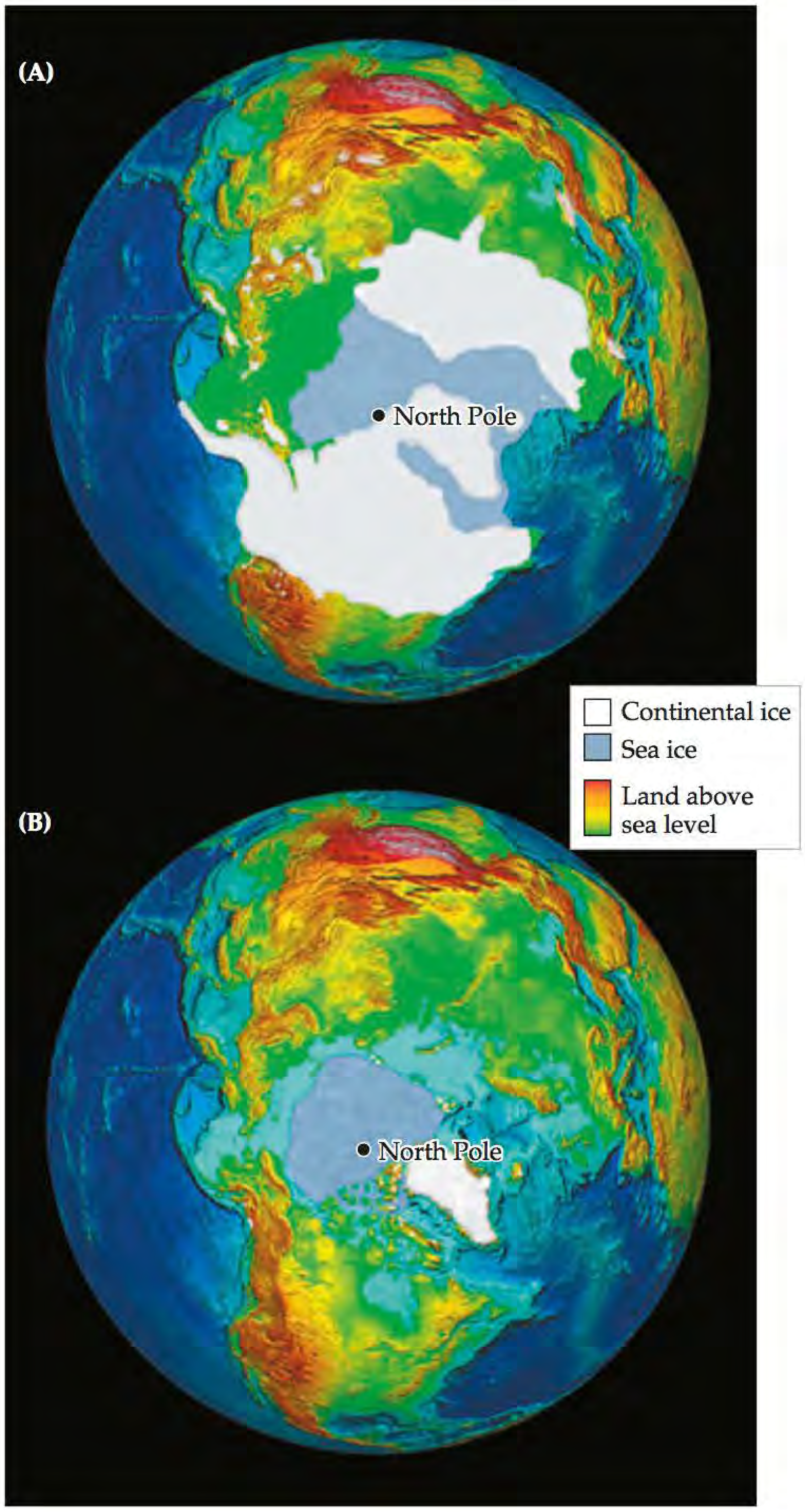
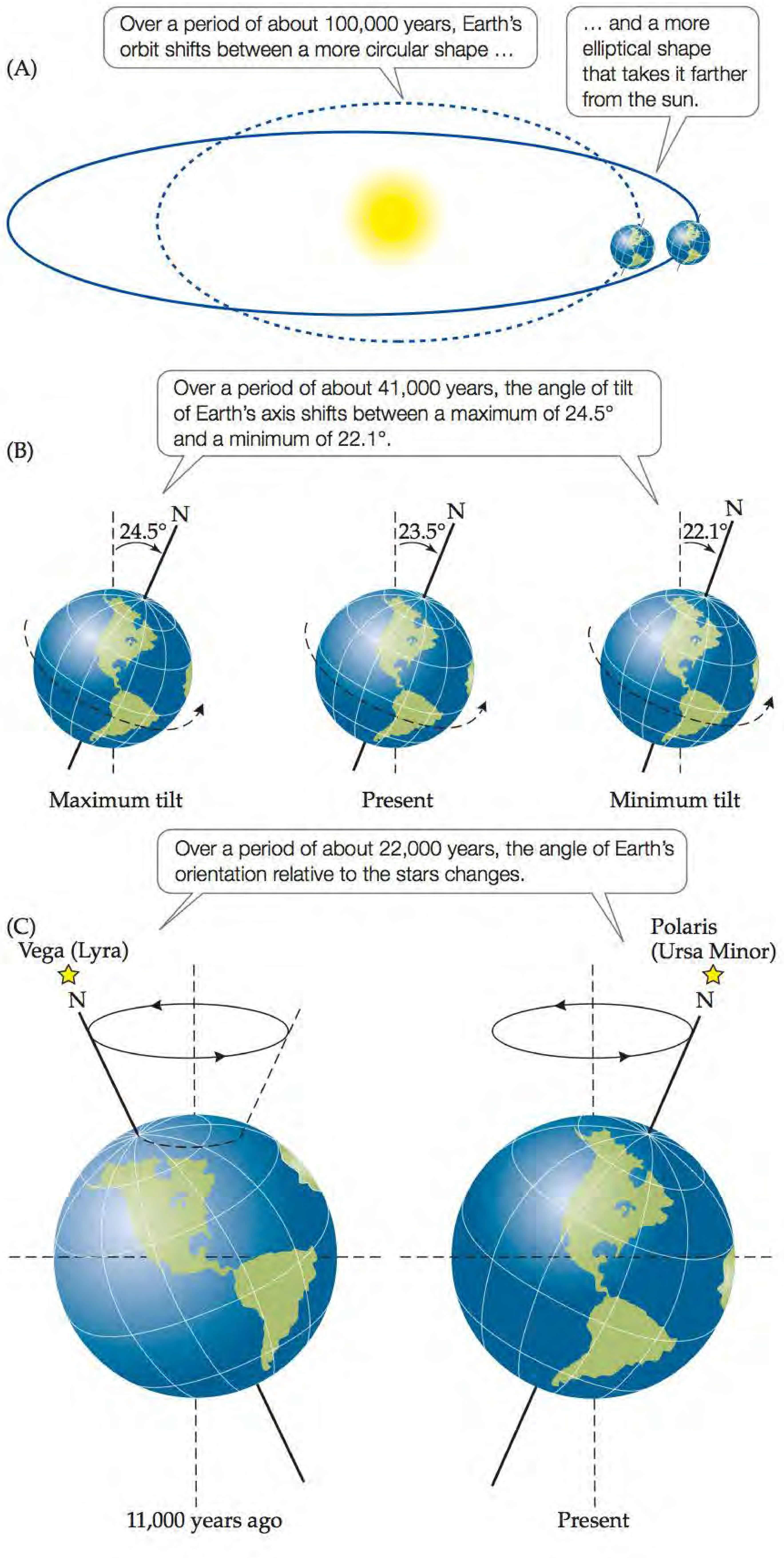


Figure 2.25 The Most Recent Glaciation of the Northern Hemisphere (A) At the last glacial maximum, about 18,000 years ago, ice sheets covered extensive areas of the Northern Hemisphere. (B) Today's ice sheets are shown for comparison.

Figure 2.26 Milankovitch Cycles and Long-Term Climate Variation Variations in (A) the shape of Earth's orbit around the sun, (B) the tilt of Earth's axis of rotation, and (C) the orientation of the axis in relation to other celestial objects all affect the intensity and distribution of solar radiation striking Earth and correlate with glacial–interglacial cycles over the past 400,000 years.

What combination of conditions associated with these three cycles would promote the occurrence of a glacial period?



of glacial advance are referred to as *glacial maxima*, and the periods of glacial melting and retreat are referred to as *interglacial periods*. These glacial–interglacial cycles occur at frequencies of about 100,000 years. We are currently in an interglacial period; in the past, these periods have lasted approximately 23,000 years. The last glacial maximum was approximately 18,000 years ago (**Figure 2.25**).

What causes the regularity of these glacial–interglacial cycles? One hypothesis was proposed by the Serbian astrophysicist Milutin Milankovitch in the 1920s. He suggested that a combination of regular changes in the shape of Earth's orbit and the tilt of its axis, collectively known as **Milankovitch cycles**, changed the intensity of solar radiation at high latitudes. Currently, the shape of Earth's orbit is nearly circular, but it shifts between a circular and a more elliptical shape in regular cycles of 100,000 years (**Figure 2.26A**). When Earth has a more elliptical orbit, the distance between Earth and the sun at the aphelion is greater, and thus the intensity of solar radiation is less, accentuating seasonal variation in climate. The angle of tilt of Earth's axis of rotation also changes in regular cycles of about 41,000 years (**Figure 2.26B**): the greater the angle of tilt, the greater the seasonal variation in solar radiation at Earth's surface. Currently, the axis is tilted at an angle of 23.5°, which is near the middle of its range of variation (24.5°–22.1°). Finally, Earth's orientation relative to other celestial bodies changes in regular cycles of about 22,000 years. Today, the North Pole is oriented toward Polaris, the North Star, but that has not always been the case; there have been other "North Stars" in the past. These changes in Earth's orientation influence the timing of the seasons by determining the hemisphere that receives more solar radiation (**Figure 2.26C**).

Long-term climate cycles correlate well with the Milankovitch cycles (Hays et al. 1976). The dominant glacial–interglacial cycle has a period of 100,000 years, corresponding to the changes in the shape of Earth's orbit. Indications of smaller climate fluctuations with 41,000-year and 22,000-year cycles have also been observed.

These changes in climate over time have had profound effects on the distributions of organisms, as we will see in Chapter 3. But climate is not the only factor that determines where organisms can live. The chemical environment also plays an important role.

CONCEPT 2.6

Salinity, acidity, and oxygen concentrations are major determinants of the chemical environment.

The Chemical Environment

All organisms are bathed in a matrix of chemicals. Water is the primary chemical constituent of aquatic environments, along with variable amounts of dissolved salts and gases. Small differences in the concentrations of these dissolved chemicals can have important consequences for the functioning of aquatic organisms, as well as for terrestrial plants and microorganisms that are dependent on water and dissolved chemicals in the soil. Terrestrial organisms are immersed in a gaseous atmosphere that is relatively invariant, consisting primarily of nitrogen (78%), oxygen (20%), water vapor (1%), and argon (0.9%). The atmosphere also contains trace gases, including the greenhouse gases, which play a critical role in Earth's energy balance, and pollutants derived from human activities, which can have important effects on atmospheric chemistry. We will discuss the effects of air pollutants and greenhouse gases in Chapter 25. Here we briefly review three chemical variables that influence biological and ecological function: salinity, acidity, and the availability of oxygen.

All waters contain dissolved salts

Salinity refers to the concentration of dissolved salts in water. *Salts* are ionic compounds, composed of cations (positively charged ions) and anions (negatively charged ions) that disassociate when placed in water. Dissolved salts are important from a biological perspective because they influence properties of water that affect the ability of organisms to absorb it, as we will see in Concept 4.3. Salts also have direct influences on organisms as nutrients (as we will see in Concept 22.1) and can inhibit metabolic activity if their concentrations are too high or too low.

Although all waters contain dissolved salts, we often think about salinity in the context of oceans, which account for 97% of the water on Earth; 70% of Earth's surface is under salty ocean waters. The salinity of the oceans varies between 33 and 37 parts per thousand; this variation is a result of evaporation, precipitation, and the freezing and melting of sea ice (**Figure 2.27**). The salinity of ocean surface waters is highest near the equator and lowest at high latitudes.

What are the salts that make water saline, and where do they come from? Ocean salts consist mainly of sodium, chloride, magnesium, calcium, sulfate, bicarbonate, and potassium. These salts come from gases emitted by volcanic eruptions early in Earth's history, when its crust was cooling, and from the gradual breakdown of minerals in the rocks that make up Earth's crust.

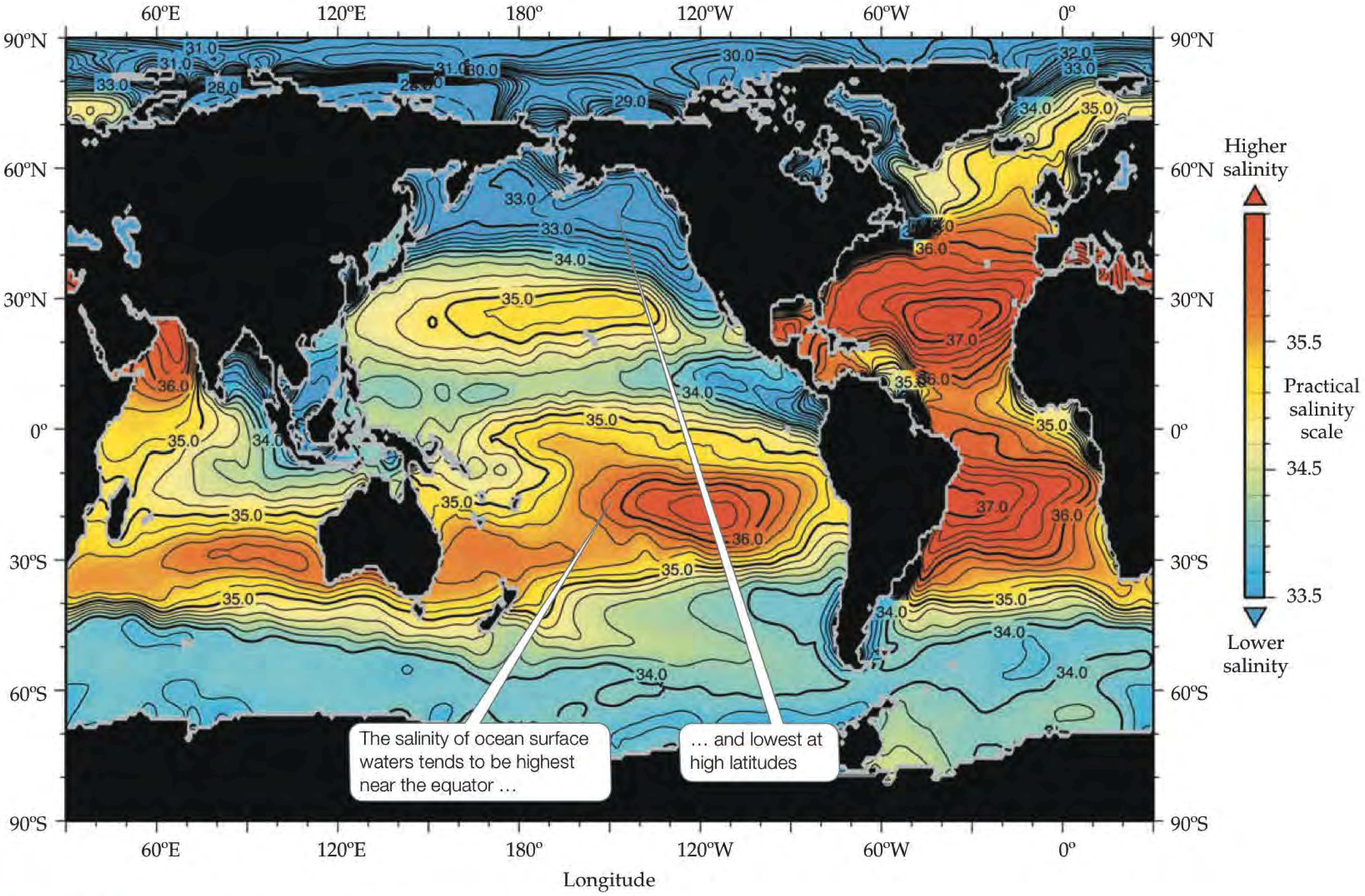
The salinity of water bodies is determined by the balance of inputs and losses of salts and water. Most landlocked bodies of water become more saline over time, reflecting a balance between water inputs from precipitation, water losses due to evaporation, and inputs of salts. When these inland "seas" occur in arid areas (e.g., the Great Salt Lake and the Dead Sea), their salinities usually exceed that of ocean water because of high rates of evaporation and its concentrating effect. The types of salts that contribute to their salinity vary, reflecting the chemistry of the minerals in the rocks that make up their basins. Despite the high salinity levels in these inland lakes, some organisms have managed to thrive in their waters, including algae and cyanobacteria.

High levels of salinity occur naturally in waterlogged soils adjacent to oceans, such as those in salt marshes. Soils may also become more saline in arid regions as water from deeper soil layers is brought to the surface by plant roots or through pumping of groundwater for irrigation. As this transported water evaporates, it leaves its salts behind. If there is little precipitation to leach the salts to deeper soil layers, or if drainage of the water is impeded by impervious layers beneath the soil, high rates of evapotranspiration will result in a progressive buildup of salts at the soil surface. This process, known as **salinization**, occurs naturally in some desert soils and is a common occurrence in irrigated agricultural soils of arid regions (**Figure 2.28**). Salinization contributed to agricultural decline in ancient Mesopotamia (now Iraq) and is a problem today in California's Central Valley, Australia, and other regions.

Organisms are sensitive to the acidity of their environment

Acidity and its converse, **alkalinity**, are measures of the ability of a solution to behave as an acid or a base, respectively. *Acids* are compounds that give up protons (H^+) to the water they are dissolved in. *Bases* take up protons or give up hydroxide ions (OH^-). Examples of common acids include the citric, tannic, and ascorbic acids found in fruits. Examples of common bases include sodium bicarbonate (baking soda) and other carbonate minerals in rock. Acidity and alkalinity are measured as pH, which is equal to the negative of the logarithm ($-\log_{10}$) of the concentration of H^+. Thus, one pH unit represents a tenfold change in the concentration of H^+. Pure water has a neutral pH of 7.0. Solutions with pH values higher than 7.0 are alkaline (basic), and solutions with pH values lower than 7.0 are acidic.

The pH values of water have important effects on organismal function. Changes in pH values can directly affect metabolic activity. The pH values of water also determine the chemistry and availability of nutrients, as we will see in Concept 22.4. Organisms have a limited range of pH values that they can tolerate. Natural levels of alkalinity (when the pH of the environment exceeds 7) tend not to be as important as levels of acidity as a constraint on organismal function and distributions.



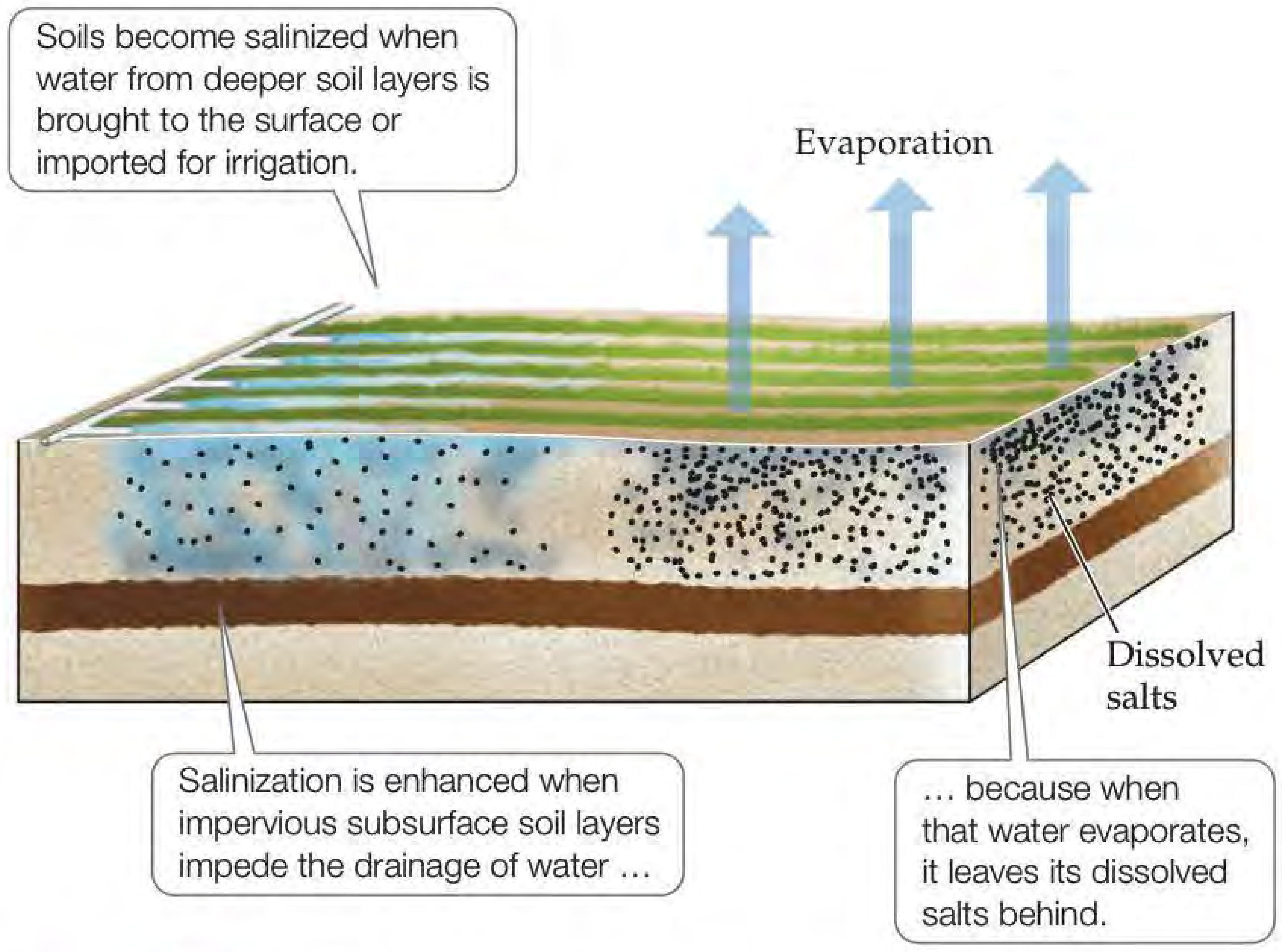
The salinity of ocean surface waters tends to be highest near the equator …

… and lowest at high latitudes

Figure 2.27 Global Variation in Salinity at the Ocean Surface Variations in the salinity of ocean surface waters reflect the concentrating effect of evaporation, dilution by melting sea ice, and precipitation.

In the oceans, pH does not vary appreciably, because the chemistry of seawater *buffers* changes in pH—that is, the salts in seawater bind free protons and thereby minimize changes in pH. Thus, pH tends to be more variable in terrestrial and freshwater ecosystems than in the ocean. Increases in atmospheric CO_2 concentrations due to human activities are increasing the acidity of the oceans with negative effects on marine ecosystems. Marine animals that build shells using calcium carbonate are less able to construct and maintain their shells under more acidic conditions (Orr et al. 2005). We will discuss this phenomenon more thoroughly in Concept 25.1.

On land, the pH of surface waters and soils varies naturally. What causes this variation? Water can become more acidic over time through the input of acidic compounds derived from several sources, most associated with soil development (which is covered in more detail in Concept 22.1). Two of the main components of soil are mineral particles from the breakdown of rocks, and



Soils become salinized when water from deeper soil layers is brought to the surface or imported for irrigation.

Salinization is enhanced when impervious subsurface soil layers impede the drainage of water …

… because when that water evaporates, it leaves its dissolved salts behind.

Figure 2.28 Salinization Salinization of soils is disrupting agricultural production in many areas, especially in arid regions.

organic matter from the decomposition of dead plants and other organisms. Some rock types, such as granites, generate acidic salts, while other rock types, such as limestones, generate basic salts. Soils become more acidic as they age because the basic salts leach away more easily and because decomposition and leaching of plant matter adds organic acids to the soil. The emission of acidic pollutants into the atmosphere by the burning of fossil fuels, as well as overuse of agricultural fertilizers, can increase the acidity of soil and water. We will cover these sources of acidity in more detail in Concept 25.3.

Oxygen concentrations vary with elevation, diffusion, and consumption

There was no oxygen in the atmosphere when life on Earth first evolved, and oxygen was toxic to the earliest forms of life. Even today, there are organisms that are intolerant of oxygen. However, with the exception of some archaea, bacteria, and fungi, most organisms require oxygen to carry out their metabolic processes and cannot survive in **hypoxic** (low-oxygen) conditions. Hypoxic conditions can also promote the formation of chemicals (e.g., hydrogen sulfide) that are toxic to many organisms. In addition, oxygen levels are important for chemical reactions that determine the availability of nutrients.

Oxygen concentrations in the atmosphere have been stable at about 21% for the past 65 million years, so most terrestrial environments have invariant oxygen concentrations. However, the availability of atmospheric oxygen decreases with elevation above sea level. As we have seen, the overall density of air decreases with elevation, so there are fewer molecules of oxygen in a given volume of air at higher elevations. We will discuss the repercussions of this variation for human health in Concept 4.1.

Oxygen concentrations can vary substantially in aquatic environments and in soils. The rate of diffusion of oxygen into water is slow and may not keep pace with its consumption by organisms. Waves and currents mix oxygen from the atmosphere into ocean surface waters, so its concentration is usually stable there. Oxygen concentrations are low in the deep ocean and in marine sediments, where biological uptake is greater than replenishment from surface waters. The same holds true in deep lakes, lake sediments, and flooded soils (e.g., in wetlands). Oxygen concentrations are highest in freshwater ecosystems with moving water (streams and rivers) because mixing with the atmosphere is greatest there.

A CASE STUDY REVISITED

Climate Variation and Salmon Abundance

The research of Steven Hare and Robert Francis on salmon production in the North Pacific contributed to the discovery of the Pacific Decadal Oscillation. As noted earlier, the

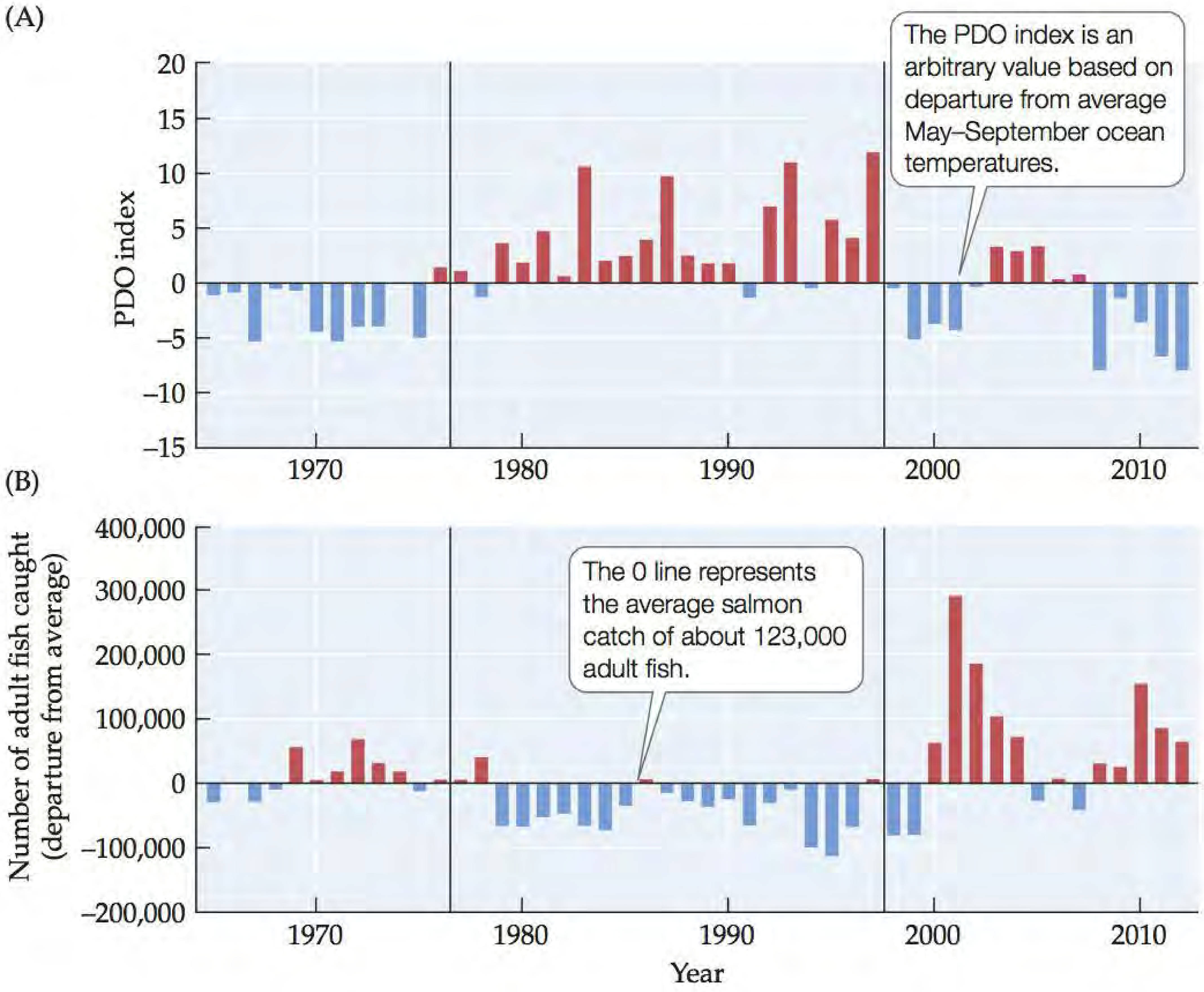


Figure 2.29 Effect of the PDO on Salmon Catch in the Northwest United States (A) Summer average PDO index, 1965–2012. Red and blue bars indicate ocean temperatures that are warmer or cooler than average, respectively. (B) Departures from the average (123,131 fish) in numbers of adult Chinook salmon returning to the Columbia River (Washington and Oregon) to spawn, 1965–2012. (After Peterson et al. 2013.)

? How frequently does the cool phase of the PDO correspond to a greater than average catch of salmon? Conversely, how often does a warm phase of the PDO correspond to a lower than average catch of salmon?

TABLE 2.1 Summary of Climate Effects of the Pacific Decadal Oscillation (PDO)

CLIMATE EFFECT	WARM PHASE PDO	COOL PHASE PDO
Ocean surface temperature in the northeastern and tropical Pacific	Above average	Below average
October–March northwestern North American air temperature	Above average	Below average
October–March southeastern U.S. air temperature	Below average	Above average
October–March southern U.S./northern Mexico precipitation	Above average	Below average
October–March northwestern North American and Great Lakes precipitation	Below average	Above average
Northwestern North American spring snowpack and water year (October–September stream flow)	Below average	Above average
Winter and spring flood risk in the Pacific Northwest	Below average	Above average

Source: Mantua 2001.

PDO is a multi-decadal shift in sea surface temperature and atmospheric pressure cells. A review of existing records of sea surface temperatures over the past century indicated that the PDO was associated with alternating 20- to 30-year periods of warm and cool temperatures in the North Pacific (**Figure 2.29A**). The length of the phases of the PDO differentiates it from other climate oscillations, whose phases tend to be much shorter (e.g., 18 months–2 years for ENSO). The warm and cool phases of the PDO influenced the marine ecosystems that Pacific salmon depended on, and thus shifted salmon production north or south, depending on the phase (**Figure 2.29B**).

The PDO has been linked to changes in the abundances and distributions of many marine organisms and, through its climate effects, changes in the functioning of terrestrial ecosystems (Mantua and Hare 2002). Its effects have been found primarily in western North America and eastern Asia, but effects have also been reported in Australia. Thus, the influence of the PDO on climate extends throughout the Western Hemisphere. Evidence for the existence of climate changes associated with the PDO dates back to the 1850s, in the form of instrumental temperature records, and to the 1600s, in the form of information from corals and tree rings. The mechanisms underlying the PDO are unclear, but its effect on climate is significant and widespread (**Table 2.1**).

CONNECTIONS IN NATURE
Climate Variation and Ecology

Two aspects of the PDO are particularly important in the context of ecology. First, the realization that the PDO existed was driven initially by an attempt to understand variation in the size of an animal population. This observation underscores the relationship between physical conditions (the topic of this chapter), the functioning of individual organisms and their growth and reproduction (Chapters 4 and 5), and population and community processes (Units 2 and 5, respectively). This relationship is one of the central themes of ecology that will form a common thread throughout this book. Ultimately, the physical environment, including climate and the myriad factors, such as the PDO, that control it, determines whether an organism can exist in a given location (as we'll see in Chapter 3). Extremes in the physical environment, including those that are driven by climate oscillations, play a critical role in our understanding of ecological phenomena.

Second, the time scale of the climate variation associated with the PDO is long relative to the human life span. The abrupt changes in climate, and the associated ecological responses of the marine ecosystem, were therefore perceived by people as unusual events. Indeed, the phases of the PDO may be longer than the life spans of most of the organisms affected by it, limiting their ability to adapt to this climate oscillation. As a result, from the perspective of an ecological community, the PDO represents a disturbance, an event that detrimentally affects the populations of some species and disrupts the community.

Although we don't yet understand what causes it, the PDO has been a part of the climate system for at least the last 400 years. A better understanding of its effects will help us place other climate phenomena, including global climate change, in perspective.

Summary

CONCEPT 2.1 Climate is the most fundamental component of the physical environment.

- Weather refers to the current conditions of temperature, precipitation, humidity, wind, and cloud cover. Climate is the long-term average weather at a given location.
- Climate determines the geographic distribution and physiological functioning of organisms.
- The climate system is driven by the balance between energy gains from solar radiation and reradiation by the atmosphere and energy losses due to infrared radiation from Earth's surface, latent heat flux, and sensible heat flux.

CONCEPT 2.2 Winds and ocean currents result from differences in solar radiation across Earth's surface.

- Latitudinal differences in the intensity of solar radiation at Earth's surface establish atmospheric circulation cells.
- The Coriolis effect and the difference in heat capacity between the oceans and the continents act on atmospheric circulation cells to determine the pattern of prevailing winds at Earth's surface.
- Ocean currents are driven by surface winds and by differences in water temperature and salinity.
- Winds and ocean currents transfer energy from the tropics to higher latitudes.

CONCEPT 2.3 Large-scale atmospheric and oceanic circulation patterns establish global patterns of temperature and precipitation.

- Global temperature patterns are determined by latitudinal variation in solar radiation, but they are also influenced by oceanic circulation patterns and by the distribution of continents.
- Temperature decreases as the elevation of the land surface increases.
- Global patterns of terrestrial precipitation are determined by atmospheric circulation cells, but they are also influenced by semipermanent pressure cells.

CONCEPT 2.4 Regional climates reflect the influence of oceans and continents, mountains, and vegetation.

- Seasonal variation in temperature is greater in the middle of a continent than on the coast because ocean water has a higher heat capacity than land.
- Mountains force air masses passing over them to rise and drop most of their moisture as precipitation, resulting in moister environments on windward slopes and drier environments on leeward slopes.
- Vegetation influences regional climates through its effects on energy exchange associated with albedo, evapotranspiration (latent heat transfer), and surface winds (sensible heat transfer).

CONCEPT 2.5 Seasonal and long-term climate variation are associated with changes in Earth's position relative to the sun.

- The tilt of Earth's axis as it orbits the sun causes seasonal temperature changes in temperate and polar regions and precipitation changes in tropical regions.
- Temperature-induced differences in water density result in nonmixing layers of water in oceans and lakes. In temperate-zone lakes, these layers break down in fall and spring, allowing the movement of oxygen and nutrients.
- Variations in climate over years to decades are caused by cyclic changes in atmospheric pressure cells. These changes have widespread effects beyond the regions where the pressure cells are located.
- Long-term climate cycles over hundreds and thousands of years are associated with changes in the shape of Earth's orbit, the angle of tilt of its axis, and Earth's orientation relative to other celestial bodies.

CONCEPT 2.6 Salinity, acidity, and oxygen concentrations are major determinants of the chemical environment.

- The salinity of Earth's waters, including water in soils, is determined by the balance between inputs of salts and gains (by precipitation) and losses (by evaporation) of water.
- The pH of soils and surface waters is determined by inputs of salts from the breakdown of rock minerals, organic acids from plants, and acidic pollutants.
- Oxygen concentrations are stable in most terrestrial ecosystems, but oxygen availability decreases as elevation increases. Concentrations of oxygen in aquatic ecosystems are low where its consumption by organisms exceeds its slow rate of diffusion into water.

Review Questions

1. Why is the variability of physical conditions potentially more important than average conditions as a determinant of ecological patterns, such as species distributions?
2. Describe the factors that determine the major latitudinal climate zones (the tropic, temperate, and polar zones).
3. Why are deserts more prone to salinization from irrigation than areas with greater precipitation?

Hone Your Problem-Solving Skills

As we will see in Chapter 3, information presented in this chapter describing variation in climate can be useful in predicting where specific collections of plant types can be found. For the following descriptions, draw a graph that portrays the following important climate features.

1. Draw a graph that shows the seasonal change in temperature for both the center of the Australian continent and the center of Eurasia, with time (12 months) on the *x* axis and temperature on the *y* axis. Use Figure 2.15 as a guide, and don't worry about the actual temperatures, but instead focus on the magnitude of the seasonal change.
2. Construct a graph showing the rain-shadow effect (see Figure 2.18) along a west coast in the Northern Hemisphere. Use distance for the *x* axis, spanning a location near the coastline, moving into a mountain range, and ending on the eastern side of the mountain, indicating where each is along the *x* axis. Use both annual average temperature and precipitation on the *y* axis.
3. Graph the trend in annual precipitation for northern Mexico in an average year and for an El Niño year (see Figure 2.23 C,D); use time on the *x* axis and precipitation on the *y* axis (hint: use Figure 2.21 as a guide).

ON THE COMPANION WEBSITE

ecology4e.sinauer.com

The website includes companions to all of the Analyzing Data exercises, Online Quizzes, Flashcards, Suggested Readings, and more. In addition, the following resources are available for this chapter:

Hands-On Problem Solving

2.1 Long, Long Ago in a Galaxy Not Far Away: Seasonal Climate Variation and Axial Tilt on Habitable Planets

Online Climate Change Connection

2.1 The Importance of Extreme Events to Ecological Responses to Climate Change

3 The Biosphere

KEY CONCEPTS

CONCEPT 3.1 Terrestrial biomes are characterized by the growth forms of the dominant vegetation.

CONCEPT 3.2 Biological zones in freshwater ecosystems are associated with the velocity, depth, temperature, clarity, and chemistry of the water.

CONCEPT 3.3 Marine biological zones are determined by ocean depth, light availability, and the stability of the bottom substrate.

The American Serengeti—Twelve Centuries of Change in the Great Plains: A Case Study

Today, the region covering the central part of North America, known as the Great Plains, bears little resemblance to the Serengeti Plain of Africa. Biological diversity is very low in many parts of the current landscape, which contains large stands of uniform crop plants (which are often even genetically identical) and a few species of domesticated herbivores. In the Serengeti, on the other hand, some of the largest and most diverse herds of wild animals in the world roam a picturesque savanna (**Figure 3.1**). If not for a series of important environmental changes, however, the two ecosystems might look superficially very similar.

Biological communities in the temperate and polar zones have been subjected to natural, long-term climate change, which has led to latitudinal or elevational shifts in their positions and species composition. Eighteen thousand years ago, at the last glacial maximum of the Pleistocene epoch, ice sheets covered the northern portion of North America. Over the next 12,000 years, the climate warmed and the ice receded. Vegetation followed the retreating ice northward and colonized the newly exposed substrate. Grasslands in the center of the continent expanded into former spruce and aspen woodlands. These grasslands contained species of grasses, sedges, and low-growing herbaceous plants similar to those found in the natural grasslands that exist today.

The animal inhabitants of those earlier grasslands were, however, strikingly different from today's. A diverse collection of *megafauna* (animals larger than 45 kg, or 100 pounds) existed in North America, rivaling the diversity found today in the Serengeti (Martin 2005) (**Figure 3.2**). Thirteen thousand years ago—a relatively short time in an evolutionary context—North American herbivores included woolly mammoths and mastodons (relatives of elephants), as well as several species of horses, camels, and giant ground sloths. Predators included saber-toothed cats with 18 cm (7-inch) incisors, cheetahs, lions, and giant short-faced bears that were larger and faster than grizzly bears.

About 10,000–13,000 years ago, as the extensive grasslands of the Great Plains were developing, many of the large mammals of North America suddenly went extinct (Barnosky et al. 2004). The rapidity of the disappearance of approximately 28 genera (40–70 species) made this extinction unlike any previous extinction event during the previous 65 million years. Another unusual aspect of this extinction was that nearly all the animals that went extinct belonged to the same group: large mammals. The causes of this extinction are a mystery.

Several hypotheses have been proposed to account for the disappearance of the North American megafauna. Changes in the climate during the extinction period were rapid and could have led to changes in habitat or food supply that would have negatively affected the animals. Another hypothesis, which has generated

Figure 3.1 The Serengeti Plain of Africa Large, diverse herds of native animals migrate across the Serengeti in search of food and water.

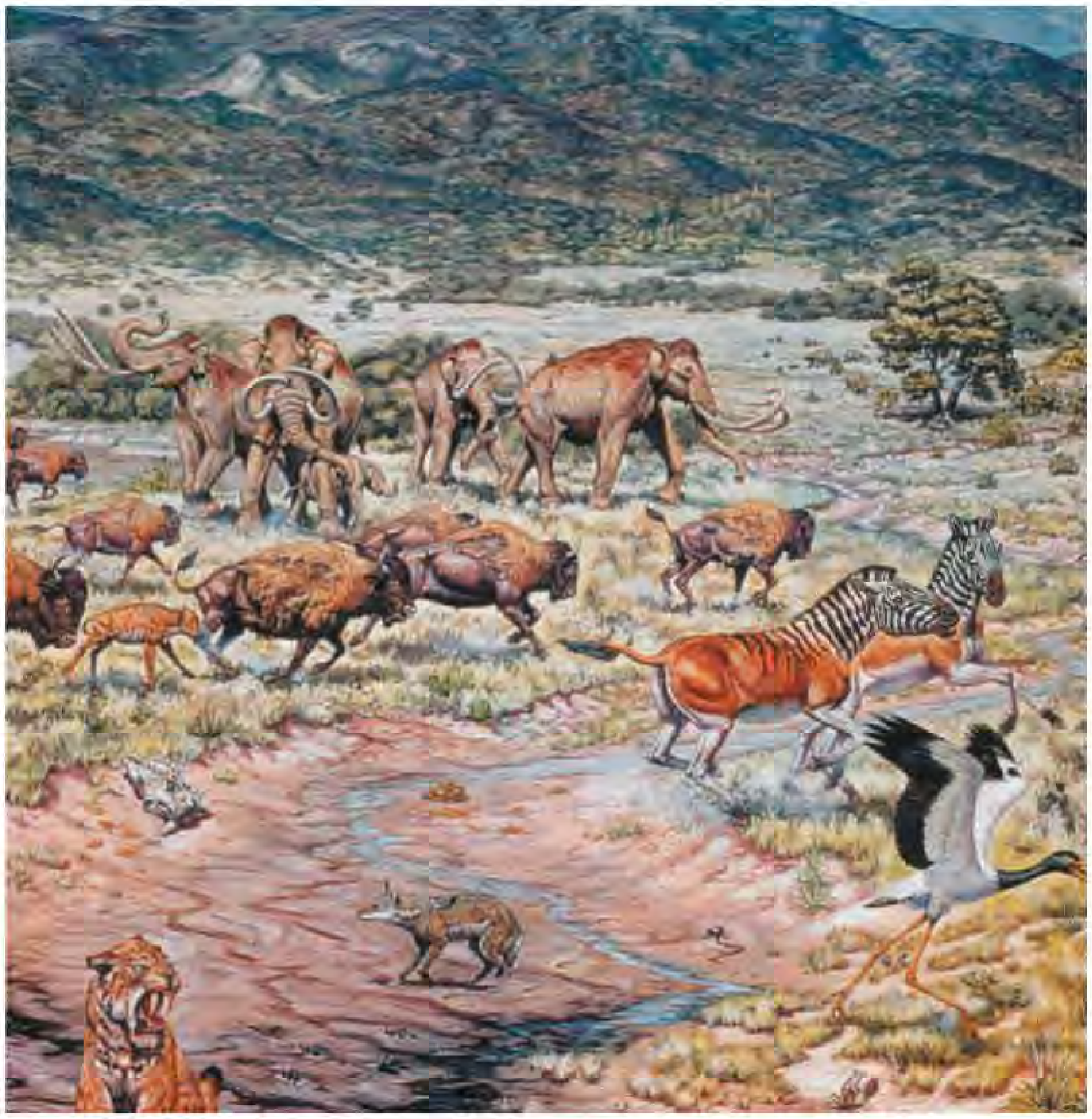


Figure 3.2 **Pleistocene Animals of the Great Plains**
The animals of the grasslands of central North America 13,000 years ago included woolly mammoths, horses, and giant bison. Many of these large mammals went extinct within a short time between 13,000 and 10,000 years ago.

substantial controversy, suggests that the arrival of humans in North America may have hastened the demise of the animals (Martin 1984). When this hypothesis was first proposed, it was met with widespread skepticism, and the initial supporting evidence was considered weak. Although humans first appeared in the central part of North America about 14,000 years ago, it is unclear how hunters bearing stone and wooden tools could have driven so many species of large mammals to extinction. What evidence is there to support the hypothesis that humans were involved in this extinction event?

Introduction

Living things can be found in remarkable places. Birds such as ravens, lammergeyers (Eurasian vultures), and alpine choughs (crows) fly over the highest summits of the Himalayas, over 8,000 m (26,000 feet) above sea level. Fish such as the "fangtooth" (*Abyssobrotula galatheae*) live more than 8,000 m below the ocean surface. Bacteria and archaea can be found almost everywhere on Earth, in hot sulfur springs at the extreme chemical and temperature limits for life, under glaciers, on dust particles many kilometers above Earth's surface, and kilometers deep in ocean sediments. However, most living things occur in a range of habitats that cover a thin veneer of Earth's surface, from the tops of trees to the surface soil layers in terrestrial environments and within 200 m of the surface of the oceans.

The **biosphere**—the zone of life on Earth—is sandwiched between the *lithosphere*, Earth's surface crust and upper mantle, and the *troposphere*, the lowest layer of the atmosphere. Biological communities can be studied at multiple scales of varying complexity, as we saw in Concept 1.2. Here, we will use the biome concept to introduce the amazing diversity of terrestrial life. The diversity of aquatic life is not as easily categorized, but we will describe several freshwater and marine biological zones, which, like terrestrial biomes, reflect the physical conditions where they are found.

CONCEPT 3.1
Terrestrial biomes are characterized by the growth forms of the dominant vegetation.

Terrestrial Biomes

Biomes are large-scale biological communities shaped by the physical environment in which they are found. In particular, they reflect the climate variation described in Chapter 2. Biomes are categorized by the most common growth forms of plants distributed across large geographic areas. The categorization of biomes does not take taxonomic relationships among organisms into account; instead, it relies on similarities in the morphological responses of organisms to the physical environment. A biome includes similar biotic assemblages on distant continents, indicating similar responses to similar climate conditions in different locations. In addition to providing a useful introduction to the diversity of life on Earth, the biome concept provides a convenient biological unit for modelers simulating the effects of environmental change on biological communities, as well as for those simulating the effects of vegetation on the climate system (see Concept 2.4). The numbers and categories of biomes used vary from source to source, depending on the preferences and goals of the authors. Here, we use a system of nine biomes: *tropical rainforest*, *tropical seasonal forest and savanna*, *desert*, *temperate grassland*, *temperate shrubland and woodland*, *temperate deciduous forest*, *temperate evergreen forest*, *boreal forest*, and *tundra*. This system provides a teaching tool for linking biological systems to the environments that shape them.

Terrestrial communities vary considerably—from the warm, wet tropics to the cold, dry polar regions. Tropical forests have multiple verdant layers, high growth rates, and tremendous species diversity. Lowland tropical forests in Borneo have an estimated 10,000 species of vascular plants, and most other tropical forest communities have about 5,000 species. In contrast, polar regions have a scattered cover of tiny plants clinging to the ground, reflecting a harsh climate of high winds, low temperatures, and dry soils. High-latitude Arctic communities contain about 100 species of vascular plants. Tropical rainforest vegetation may reach over 75 m (250 feet) in height and contain over 400,000 kg (882,000 pounds) of aboveground biomass in a single hectare (about 2.5 acres). Plants of polar regions, on the other hand, rarely exceed 5 cm (2 inches) in height and contain less than 1,000 kg (2,200 pounds) of aboveground biomass per hectare.

Terrestrial biomes are classified by the *growth form* (size and morphology) of the dominant plants (e.g., trees, shrubs, or grasses) (**Figure 3.3**). Characteristics of their leaves, such as *deciduousness* (seasonal shedding of leaves), thickness, and *succulence* (development of fleshy water storage tissues), may also be used. Why use plants rather than animals to categorize terrestrial biomes? Plants are immobile, so in order to occupy a site successfully for a long time, they must be able to cope with its environmental extremes as well as its biological pressures, such as competition for water, nutrients, and light. Plant growth forms are therefore good indicators of the physical environment, reflecting the climate zones discussed in Concept 2.2 as well as rates of disturbance (e.g., fire frequency). In addition, animals are a less visible component of most large landscapes, and their mobility allows them to avoid exposure to adverse environmental conditions. Microorganisms (archaea, bacteria, and fungi) are important components of biomes, and the composition of microbial communities reflects physical conditions as plant growth forms do. The tiny size of these organisms, however, as well as rapid temporal and spatial changes in their community composition, makes them impractical for classifying biomes.

Since their emergence from the oceans about 500 million years ago, plants have taken on a multitude of different forms in response to the selection pressures of the terrestrial environment (see Figure 3.3). These selection pressures include aridity, high and subfreezing temperatures, intense solar radiation, nutrient-poor soils, grazing by animals, and crowding by neighbors. Having

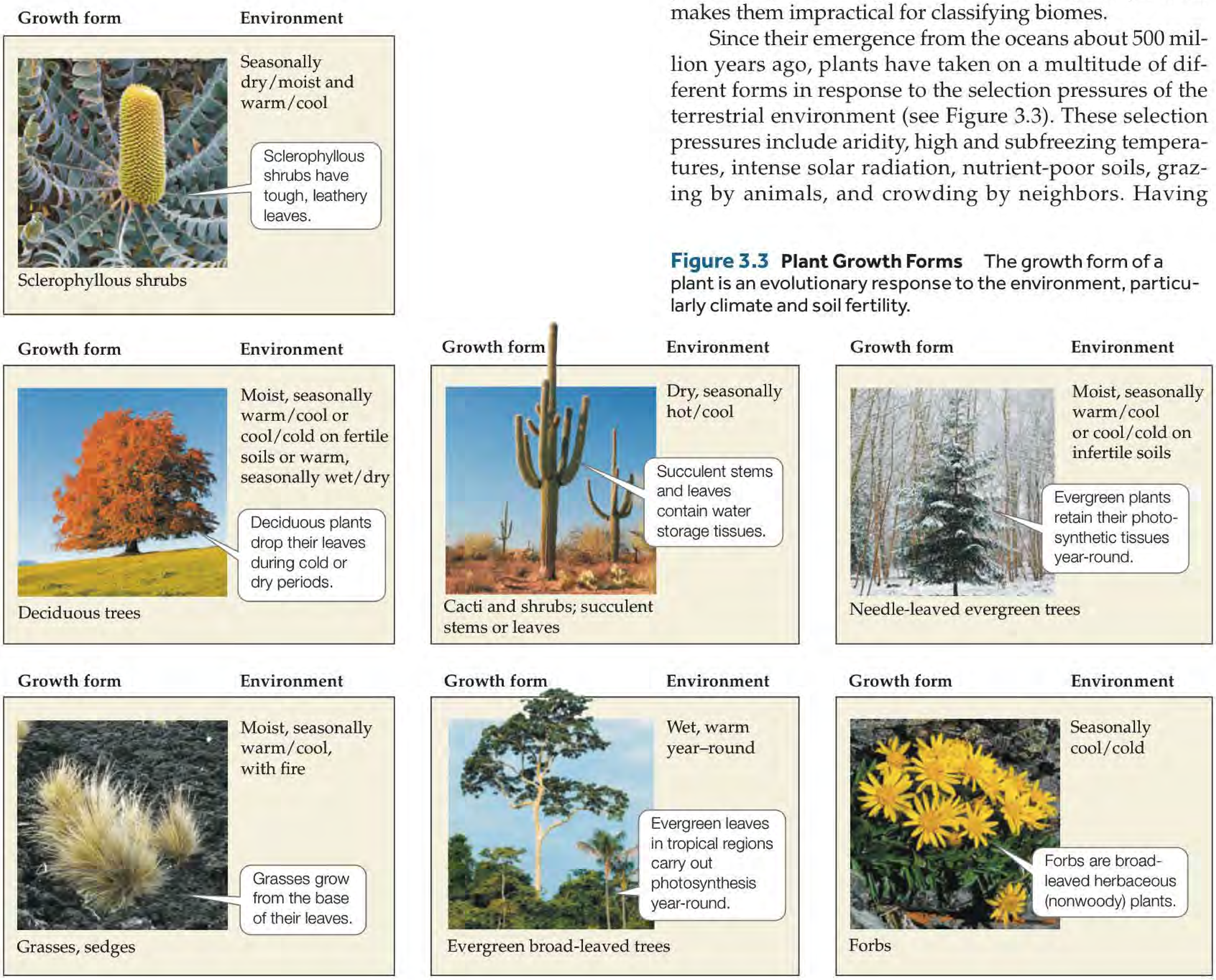


Figure 3.3 Plant Growth Forms The growth form of a plant is an evolutionary response to the environment, particularly climate and soil fertility.

deciduous leaves, for example, is one solution to seasonal exposure to subfreezing temperatures or extended dry periods. Trees and shrubs invest energy in woody tissues in order to increase their height and ability to capture sunlight and to protect their tissues from damage by wind or large amounts of snow. Perennial grasses, unlike most other plants, can grow from the bases of their leaves and keep their vegetative and reproductive buds below the soil surface, which facilitates their tolerance of grazing, fire, subfreezing temperatures, and dry soils. Similar plant growth forms appear in similar climate zones on different continents, even though the plants may not be genetically related. The evolution of similar growth forms among distantly related species in response to similar selection pressures is called **convergence**.

Terrestrial biomes reflect global patterns of precipitation and temperature

Chapter 2 described Earth's climate zones and their association with the atmospheric and oceanic circulation patterns that result from the differential heating of Earth's surface by the sun. These climate zones are major determinants of the distribution of terrestrial biomes.

The tropics (between 23.5°N and S) are characterized by high rainfall and warm, invariant temperatures. In the subtropical regions that border the tropics, rainfall becomes more seasonal, with pronounced dry and wet seasons. The major deserts of the world are associated with the zones of high pressure at about 30°N and S and with the rain-shadow effects of large mountain ranges. Subfreezing temperatures during winter are an important feature of the temperate and polar zones. The amount of precipitation north and south of 40° varies depending on proximity to the ocean and the influence of mountain ranges (see Figure 2.16).

The locations of terrestrial biomes are correlated with these variations in temperature and precipitation. Temperature influences the distribution of plant growth forms directly through its effect on the physiological functioning of plants. Precipitation and temperature act in concert to influence the availability of water and its rate of loss by plants. Water availability and soil temperature are important in determining the supply of nutrients in the soil, which is also an important control on plant growth form.

The association between climate variation and terrestrial biome distribution can be visualized using a graph of average annual precipitation and temperature (**Figure 3.4**). While these two factors predict biome distributions reasonably well, this approach fails to incorporate seasonal variation in temperature and precipitation. As we saw in Concept 2.1, climate extremes are sometimes more important in determining species distributions than average annual conditions. For example, grasslands and shrublands have wider global distributions than Figure 3.4 would suggest, occurring in regions with relatively high average annual precipitation but regular dry periods (e.g., Mediterranean-type shrublands; grasslands at the margins of deciduous forests). In addition, factors such as soil texture and chemistry as well as proximity to mountains and large bodies of water can influence biome distribution.

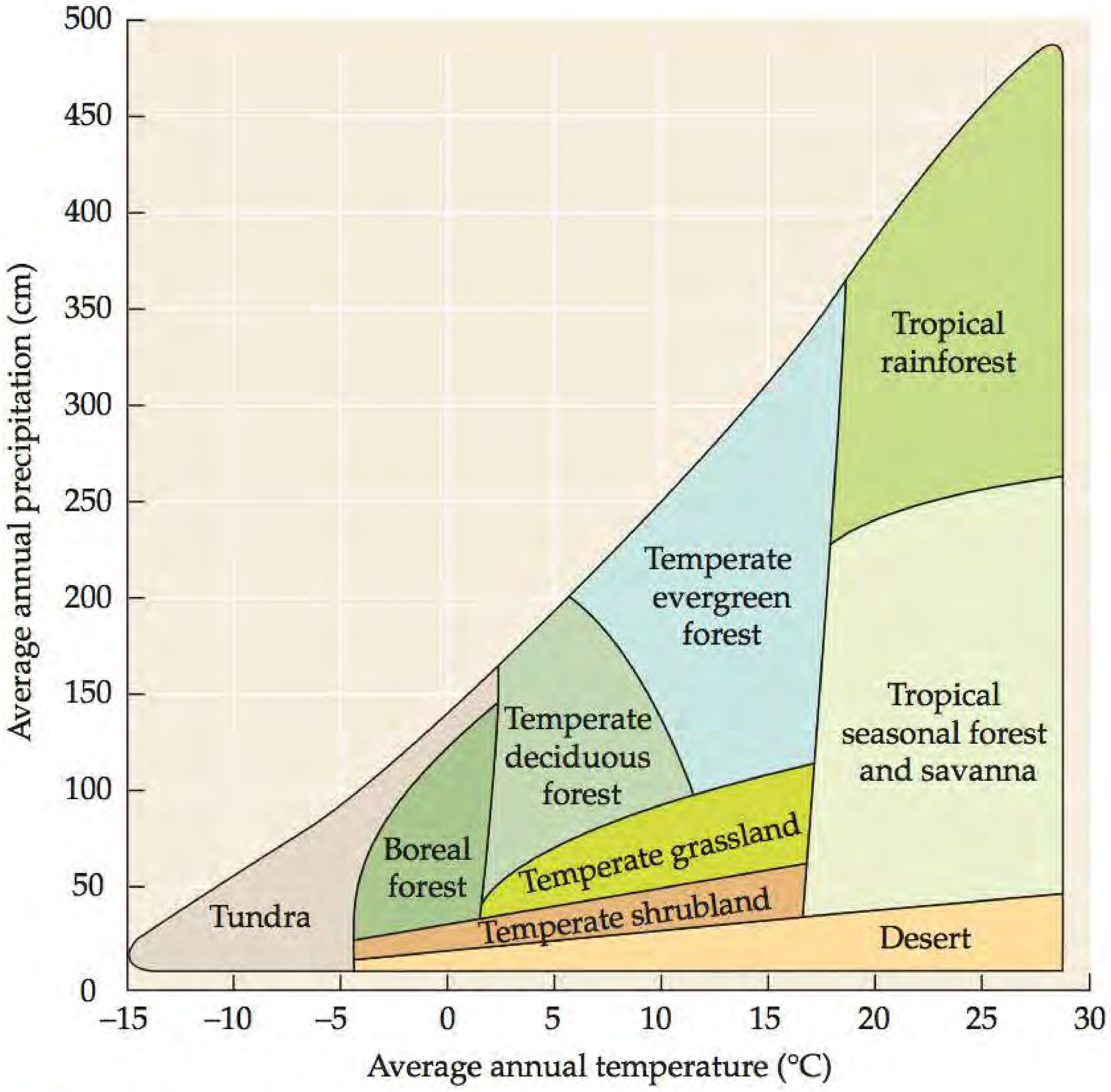


Figure 3.4 Biomes Vary with Average Annual Precipitation and Temperature When plotted on a graph of precipitation and temperature, the nine major terrestrial biomes form a triangle. (After Whittaker 1975.)

? What factor(s) might result in grasslands or shrublands "invading" climate space occupied by forest or savanna?

The potential distributions of terrestrial biomes differ from their actual distributions due to human activities

The effects of land conversion and resource extraction by humans are increasingly apparent on the land surface. These human effects are collectively described as **land use change**. Human modification of terrestrial ecosystems began at least 10,000 years ago with the use of fire as a tool to clear forests and enhance the size of game populations. The greatest changes have occurred over the last 150 years, since the onset of mechanized agriculture and logging and an exponential increase in the human population (see Figure 10.2) (Harrison and Pearce 2001). About 60% of Earth's land surface has been altered by human activities, primarily agriculture, forestry, and livestock grazing; a smaller amount (2%–3%) has been transformed by urban development and transportation corridors (Harrison and

Pearce 2001; Sanderson et al. 2002). As a result of these human influences, the potential and the actual distributions of biomes are markedly different (**Figure 3.5**). Temperate biomes, particularly grasslands, have been transformed the most, although tropical and subtropical biomes are experiencing rapid change as well.

In the following sections, we will briefly describe nine terrestrial biomes, their biological and physical characteristics, and the human activities that influence the actual amount of natural vegetation cover that remains in each biome. The description of each biome begins with a map of its potential geographic distribution and a *climate diagram* showing the characteristic seasonal patterns of air temperature and precipitation at a representative location in that biome (see **Ecological Toolkit 3.1**). In addition, sample photos illustrate some of the vegetation types

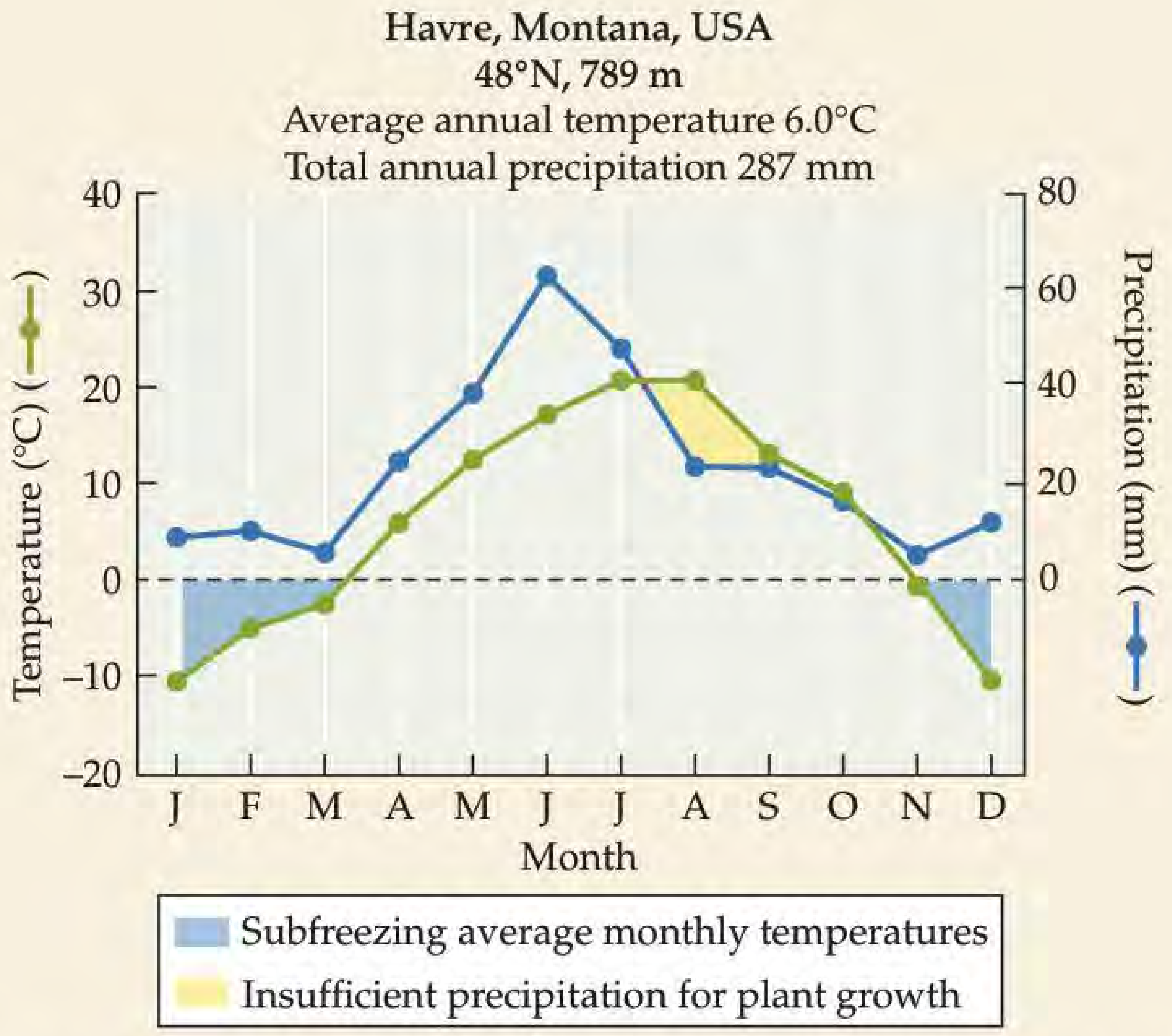
Figure 3.5 Global Biome Distributions Are Affected by Human Activities The potential distributions of biomes differ from their actual distributions because human activities have altered much of Earth's land surface. (A) The potential global distribution of biomes. (B) Alteration of terrestrial biomes by human activities. The "human footprint" is a quantitative measure (100 = maximum) of the overall human impact on the environment based on geographic data describing human population size, land development, and resource use. (B from Sanderson et al. 2002.)

? Which biomes in North America and Eurasia appear to have been most affected by human activities? In other words, which biomes in (A) overlap most with areas of high human impact in (B)? In South America and on the Indian subcontinent, which biome has been most degraded by human activity?

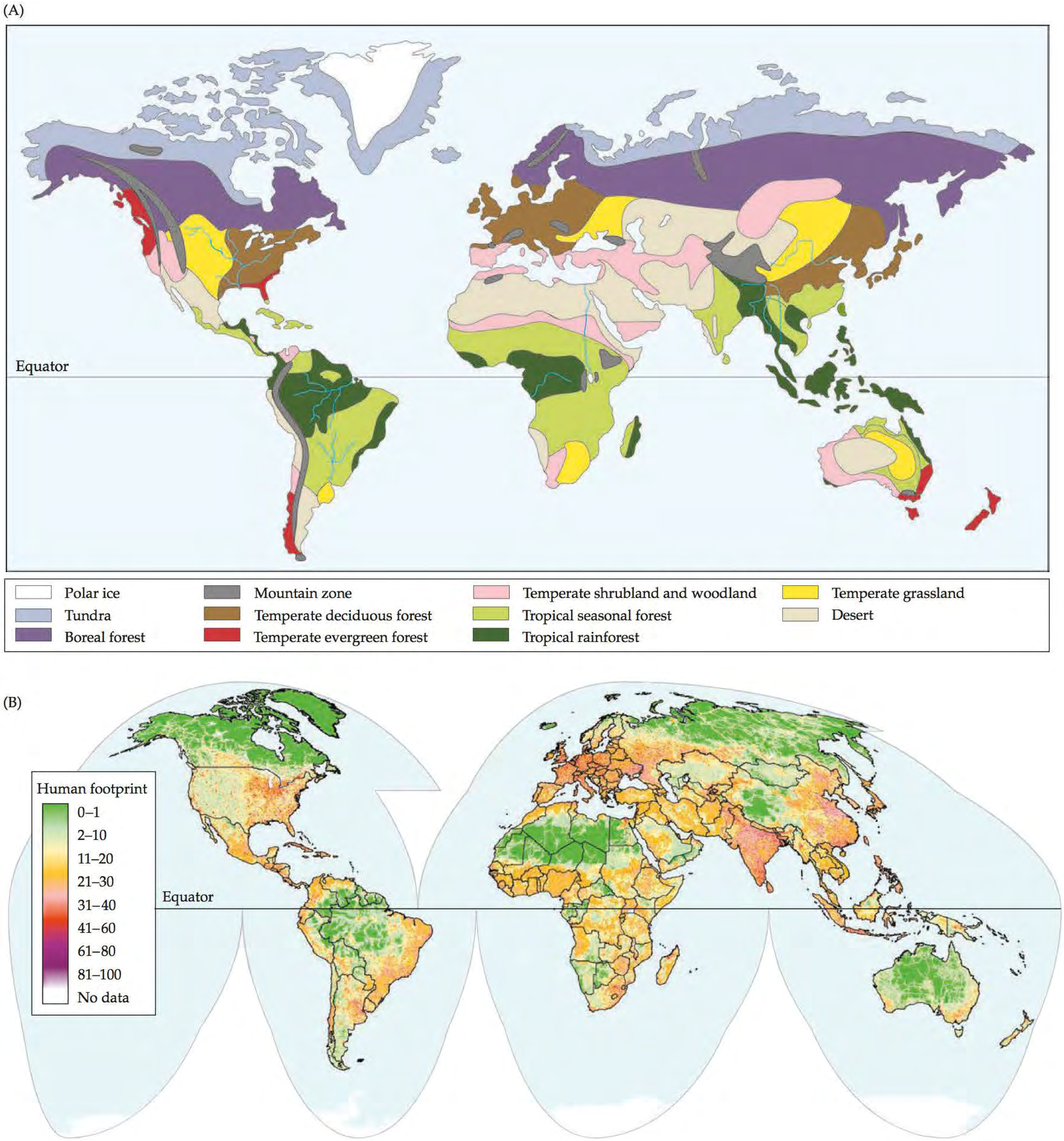
ECOLOGICAL TOOLKIT 3.1 Climate Diagrams

A climate diagram is a graph of the average monthly temperature and precipitation at a particular location. Climate diagrams are useful for depicting seasonal patterns of climate conditions. In particular, they provide an indication of when temperatures are below freezing for extended periods (blue-shaded areas in the figure) and when precipitation is insufficient for plant growth. When the precipitation curve falls below the temperature curve (yellow-shaded area in the figure), water availability limits plant growth.

Climate diagrams were developed by Heinrich Walter and Helmut Lieth (Walter and Lieth 1967), who used them to show the consistency of climate patterns within the same biomes in different locations. Walter and Lieth demonstrated that by using axes scaled with 1°C corresponding to 2 mm of precipitation, a coarse approximation of time periods when water availability limits plant growth could be made. (Water loss from terrestrial ecosystems is related to temperature, a topic we will take up in more detail in Chapter 4.) For example, the tropical seasonal forest and temperate shrubland and woodland biomes show distinct seasonal periods when water is in short supply, and some temperate grasslands also have predictable low-water seasons (see the figure). Climate diagrams also show when temperatures are conducive to plant growth. It is apparent that there is a latitudinal trend toward longer periods of subfreezing temperatures with more extreme lows (larger areas of blue shading).

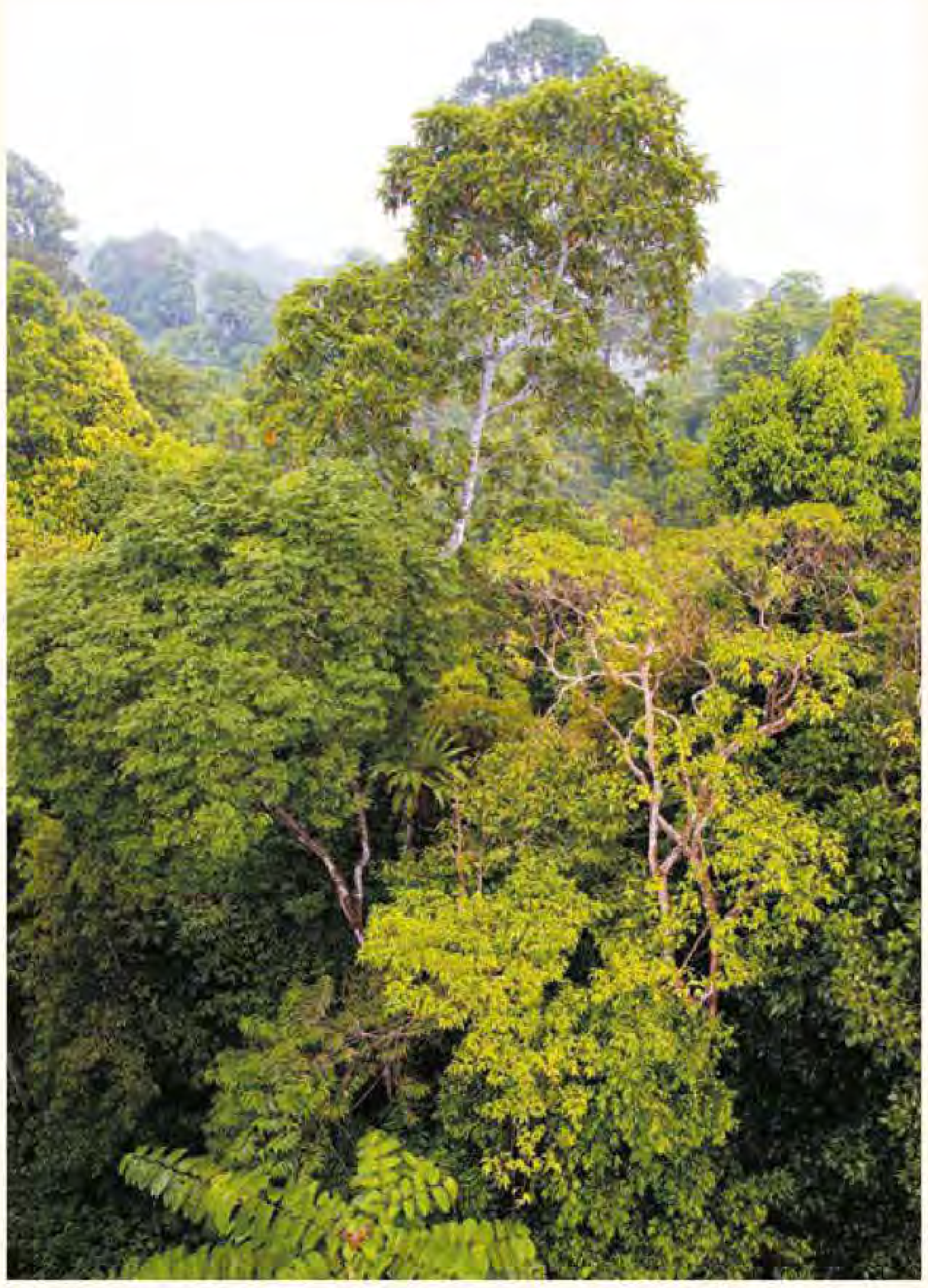


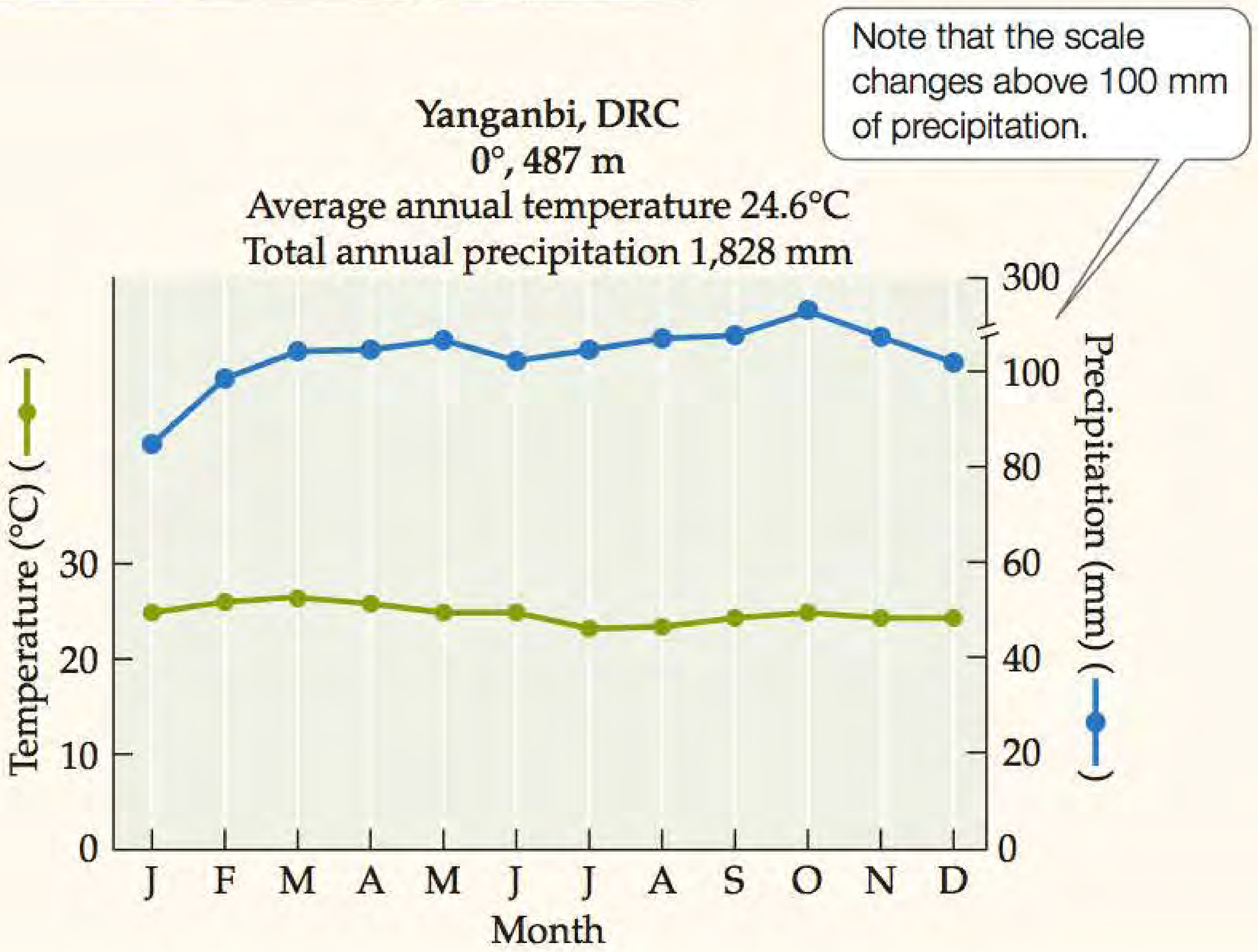
A Sample Climate Diagram A climate diagram contains the name of the climate station where conditions were recorded (Havre, Montana, in this example), its geographic location in latitude, and its elevation. In Havre, there are extended periods of subfreezing temperatures from November to March (blue areas). Frosts do occur outside this time frame, but these isolated events are not reflected in average monthly temperatures. A period of low water availability (yellow area) typically occurs from mid-July to October.


(A)
Equator
Polar ice
Tundra
Boreal forest
Mountain zone
Temperate deciduous forest
Temperate evergreen forest
Temperate shrubland and woodland
Tropical seasonal forest
Tropical rainforest
Temperate grassland
Desert
(B)
Human footprint
0–1
2–10
11–20
21–30
31–40
41–60
61–80
81–100
No data
Equator

TROPICAL RAINFORESTS


Epiphytes cling to the trunks of trees in the rainforest near Coca, Ecuador.


Multiple levels of trees form the canopy of a rainforest in Sabah, Malaysia.


Yanganbi, DRC
0°, 487 m
Average annual temperature 24.6°C
Total annual precipitation 1,828 mm

Note that the scale changes above 100 mm of precipitation.

that make up the biome. It is important to remember that each biome incorporates a mix of different communities. Boundaries between biomes are often gradual and may be complex due to variations in regional climate influences, soil types, topography, and disturbance patterns. Thus, the boundaries of biomes portrayed here are only approximations.

TROPICAL RAINFORESTS Tropical rainforests are aptly named, as they are found in the low-latitude tropics (between 10°N and S) where precipitation usually exceeds 2,000 mm (79 inches) annually. Tropical rainforests experience warm, seasonally invariant temperatures. The abundant precipitation may be spread evenly throughout the year or occur in one or two main peaks associated with the movement of the Intertropical Convergence Zone (ITCZ) (see Figure 2.21). Seasonal rhythms are generally absent from this biome, and plants grow continuously throughout the year. Tropical rainforests contain a substantial amount of living plant biomass, as mentioned earlier, and they include the most productive ecosystems on Earth. They contain an estimated 50% of Earth's species and about 37% of the terrestrial pool of carbon (C) in only about 11% of Earth's terrestrial vegetation cover (Dixon et al. 1994; Dirzo and Raven 2003). Tropical rainforests occur in Central and South America, Africa, Australia, and Southeast Asia.

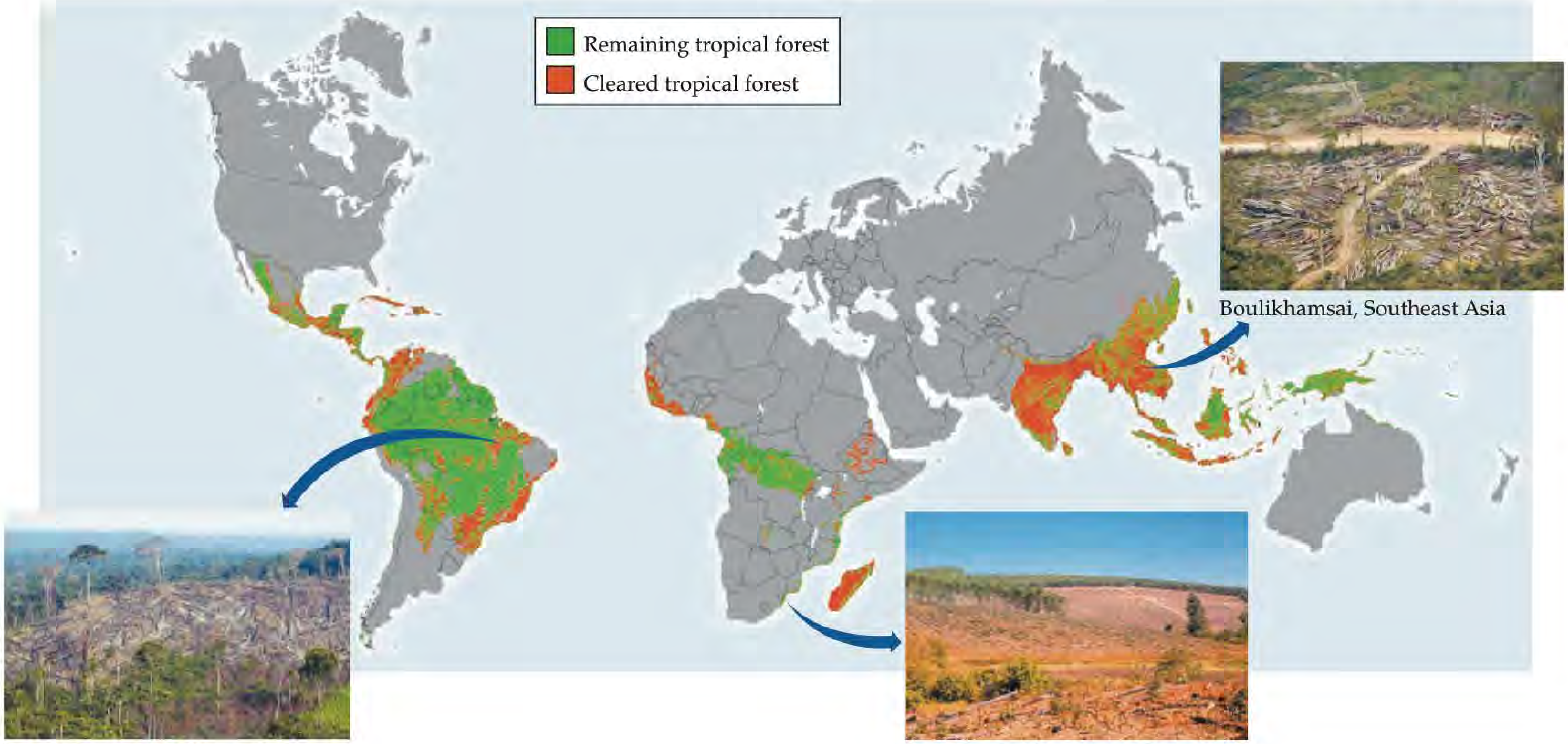


Figure 3.6 Tropical Deforestation Large areas of tropical rainforest have been cleared over the past 40 years, primarily for agricultural and pastoral development. The loss of these tropical forests has large consequences for loss of biodiversity, regional climate, and carbon uptake and storage. (Map after Pimm and Jenkins 2005.)

The tropical rainforest biome is characterized by broad-leaved evergreen and deciduous trees. Light is a key environmental factor determining the vegetation structure of this biome. Climate conditions that favor plant growth also exert selection pressure either to grow tall above neighboring plants or to adjust physiologically to low light levels. About five layers of plants occur in tropical rainforests. *Emergent trees* rise above the majority of the other trees that make up the *canopy* of the forest. The canopy consists primarily of the leaves of evergreen trees, which form a continuous layer approximately 30 to 40 m above the ground. Below the canopy, plants that use trees for support and to elevate their leaves above the ground, including *lianas* (woody vines) and *epiphytes* (plants that grow on tree branches), are found draped over or clinging to the canopy and emergent trees. *Understory* plants grow in the shade of the canopy, further reducing the light that finally reaches the forest floor. Shrubs and *forbs* (broad-leaved herbaceous plants) occupy the forest floor, where they must rely on light flecks that move across the forest floor during the day for photosynthesis.

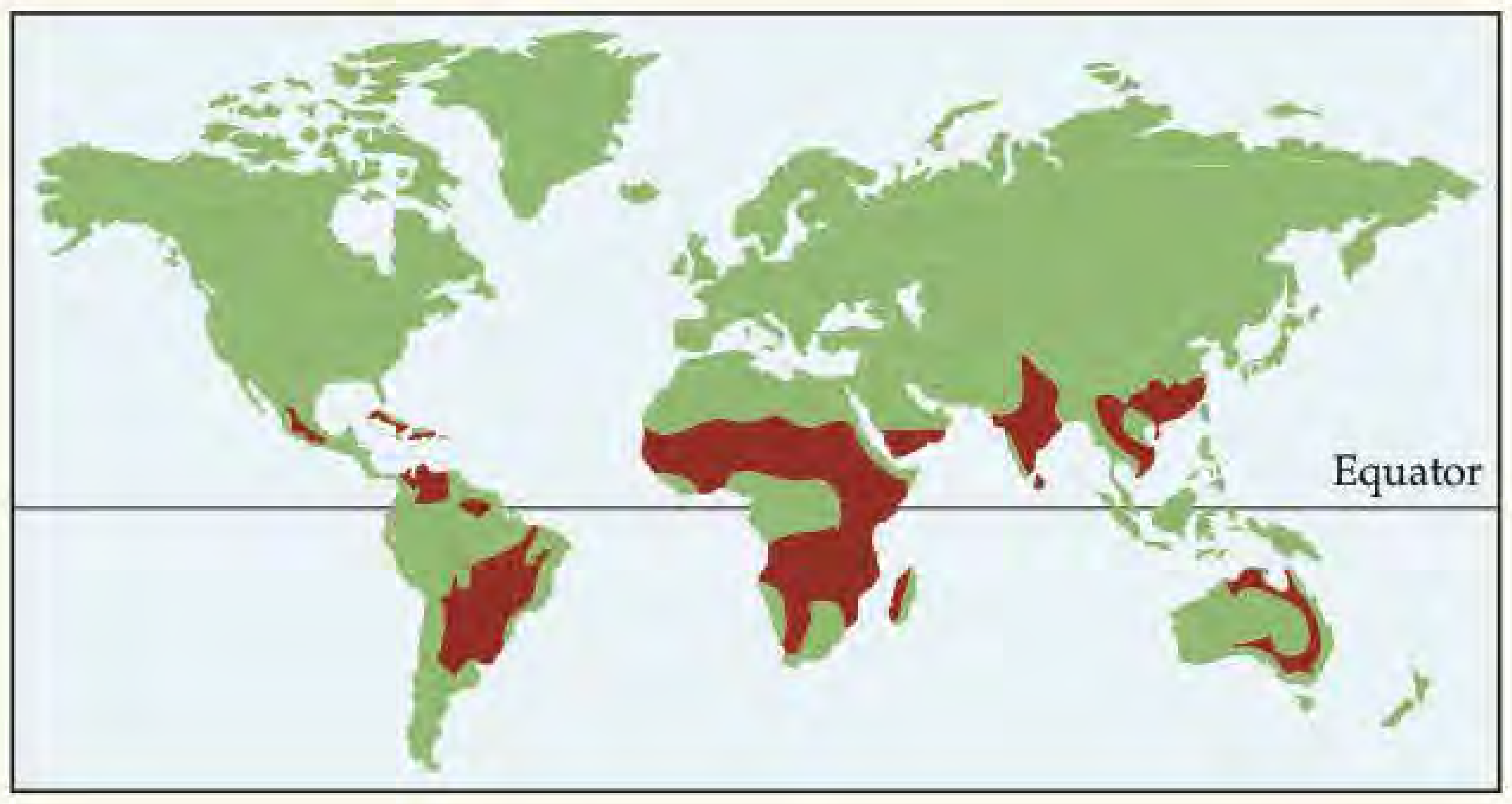
Globally, tropical rainforests are disappearing rapidly because of logging and conversion of forests to pasture and croplands (**Figure 3.6**). Approximately half of the tropical rainforest biome has been altered by deforestation (Asner et al. 2009). Rainforests in Africa and Southeast Asia have been altered the most, and rates of deforestation continue to be greatest in those areas (Wright 2005). In some cases, rainforests have been replaced by disturbance-maintained pastures of forage grasses. In other cases, rainforest is regrowing, but the recovery of the previous rainforest structure is uncertain. Rainforest soils are often nutrient-poor, and recovery of nutrient supplies may take a very long time, hindering forest regrowth.

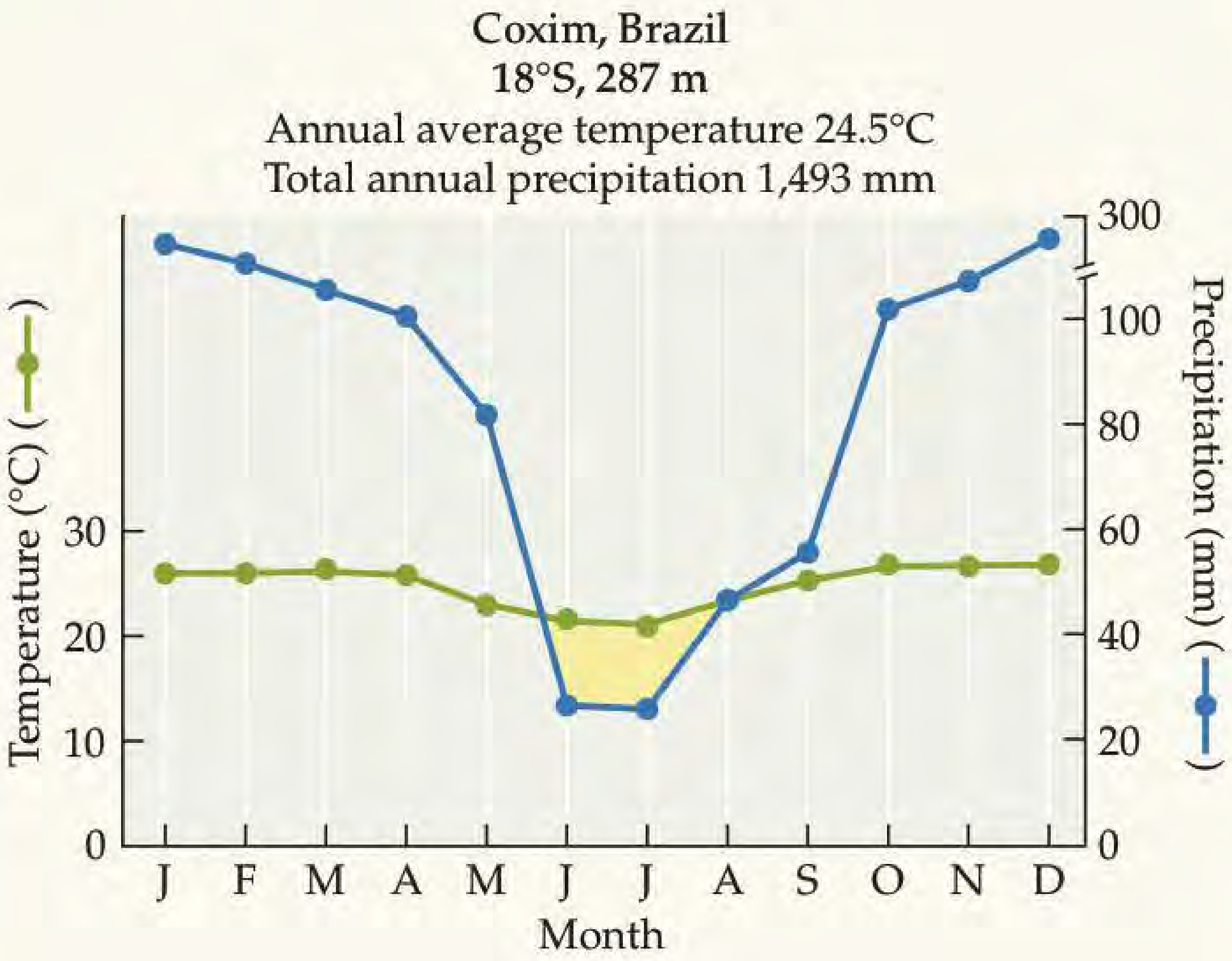
CLIMATE CHANGE CONNECTION

Tropical Forests and Greenhouse Gases The loss of tropical forests to cutting and burning means more than just the loss of biodiversity. As noted above, almost 40% of the terrestrial carbon is in the tropical forest biome. The loss of the forests means both lower ability of the terrestrial biosphere to take up C from the atmosphere and greater emissions of greenhouse gases into the atmosphere from soils and decaying vegetation (Guo and Gifford). Restoration projects are ongoing in some countries to help address concerns for the loss of diversity and C sequestration abilities associated with tropical forest loss. The Convention on Biological Diversity aims to restore 15% of degraded ecosystems by the year 2020 (Alexander et al. 2011). How quickly can tropical forests recover and the pools of C be restored once regrowth is started? A review of more than 600 sites indicates that recovery of the plant biomass above the soil surface occurs within 85 years of regrowth, but longer time is required for recovery of plant biomass in the soil (Martin et al. 2013). This analysis provides optimism for potential reversal of the contribution

TROPICAL SEASONAL FORESTS AND SAVANNAS

Baobab trees in dry season in Zambia





Semi-evergreen forest of Pijio trees (*Cavanillesia platanifolia*) during the dry season, Cerro Blanco, Ecuador

of tropical deforestation to atmospheric greenhouse gas concentrations. However, the analysis also found that while tree diversity recovers after 50 years, more than a century is required for full plant species recovery, including lianas and epiphytes.

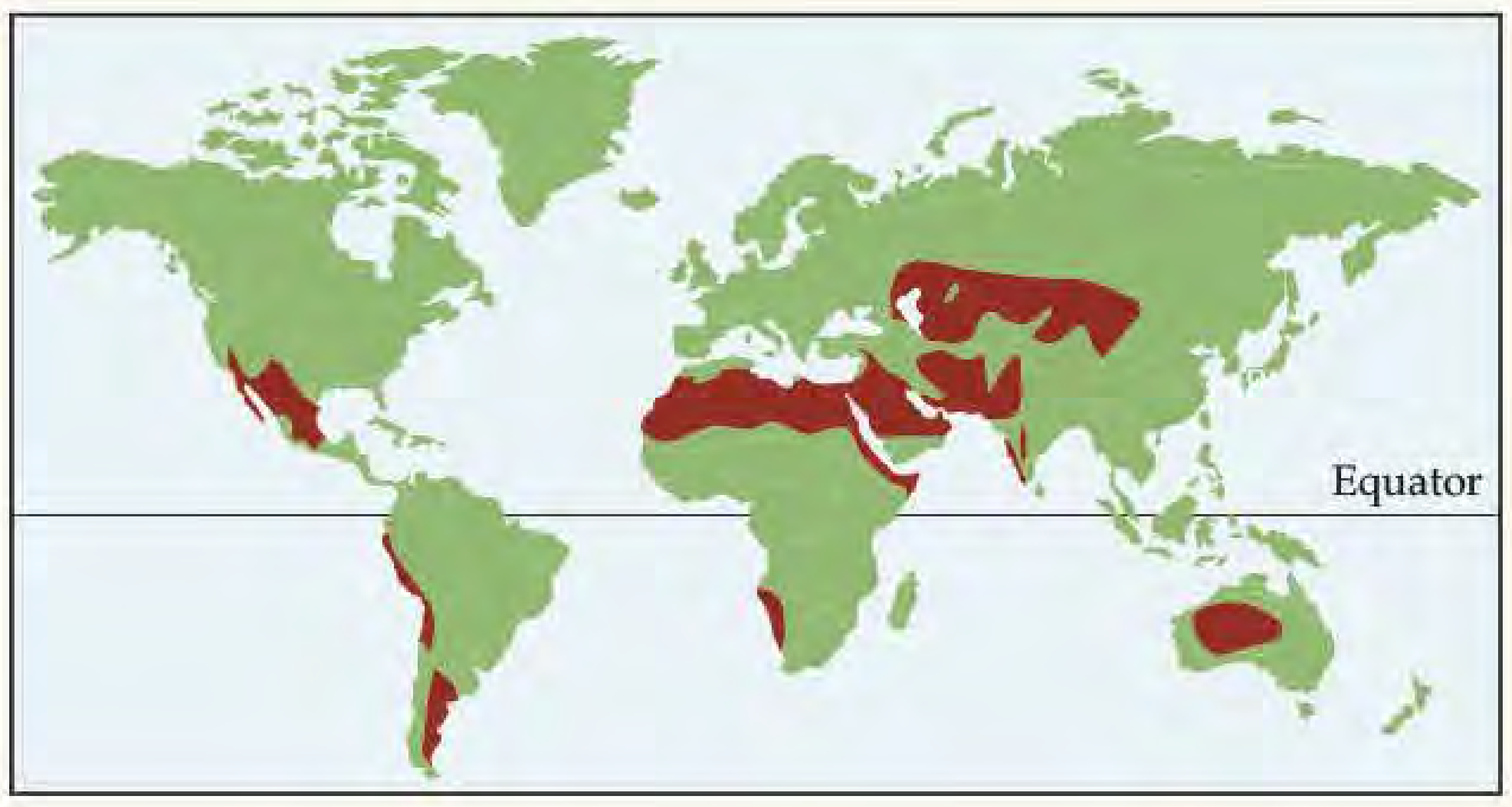
TROPICAL SEASONAL FORESTS AND SAVANNAS As we move to the north and south of the wet tropics toward the Tropics of Cancer (23.5°N) and Capricorn (23.5°S), rainfall becomes seasonal, with pronounced wet and dry seasons associated with shifts in the ITCZ. This region is marked by a large gradient in climate primarily associated with the seasonality of rainfall. The responses of vegetation to the greater seasonal variability include shorter stature, lower tree densities, and an increasing degree of drought deciduousness, with leaves dropping from the trees during the dry season. In addition, there is a greater abundance of grasses and shrubs and fewer trees than in rainforests.

The tropical seasonal biome includes several different vegetation complexes, including *tropical dry forests*, *thorn woodlands*, and *tropical savannas*. The frequency of fires, which increases with the length of the dry season, influences the vegetation growth forms. Recurrent fires, sometimes set by humans, promote the establishment of **savannas**, communities dominated by grasses with intermixed trees and shrubs. In Africa, large herds of herbivores, such as wildebeests, zebras, elephants, and antelopes, also influence the balance between trees and grasses and act as an important force promoting the establishment of savannas. On the floodplains of the Orinoco River in South America, seasonal flooding contributes to the establishment of savannas, as trees are intolerant of long periods of soil saturation. Thorn woodlands (communities dominated by widely spaced trees and shrubs) get their name from the heavy armaments of thorns on the trees, which act as a deterrent to herbivores that would consume the vegetation. Thorn woodlands typically occur in regions with climates intermediate between tropical dry forests and savannas.

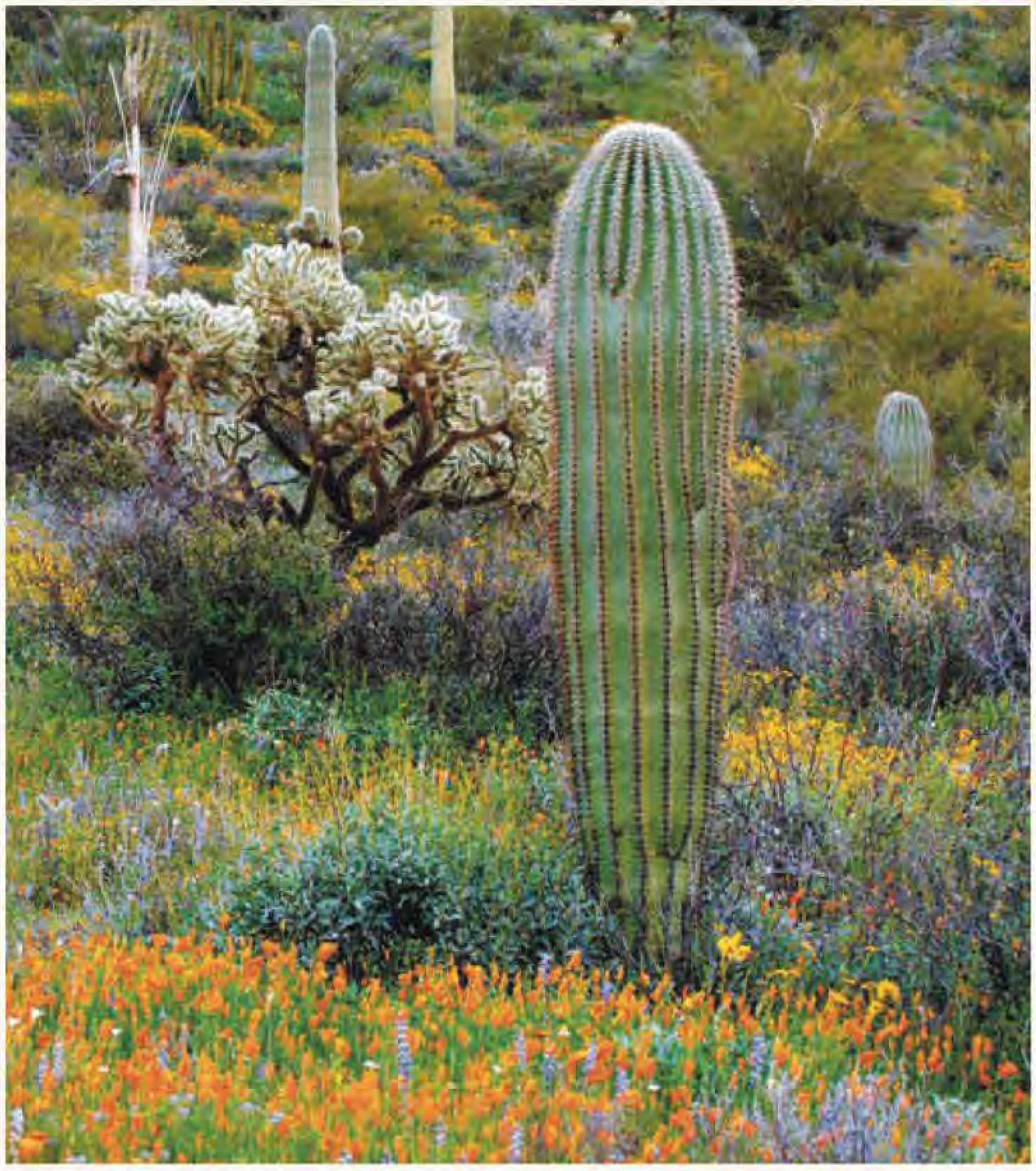
Tropical seasonal forests and savannas once covered an area greater than tropical rainforests, but today less than half of this biome remains intact. Increasing human demand for wood and agricultural land has resulted in loss of tropical seasonal forests and savannas at rates equal to or greater than those for tropical rainforests (Bullock et al. 1995). Large increases in human populations in tropical dry forest regions have had a particularly large effect. Large tracts of tropical dry forest in Asia and Central and South America have been converted to cropland and pasture to meet the needs of growing human populations for food and earnings from agricultural goods exported to more developed countries.

DESERTS In contrast to the tropical ecosystems, deserts contain sparse populations of plants and animals, reflecting

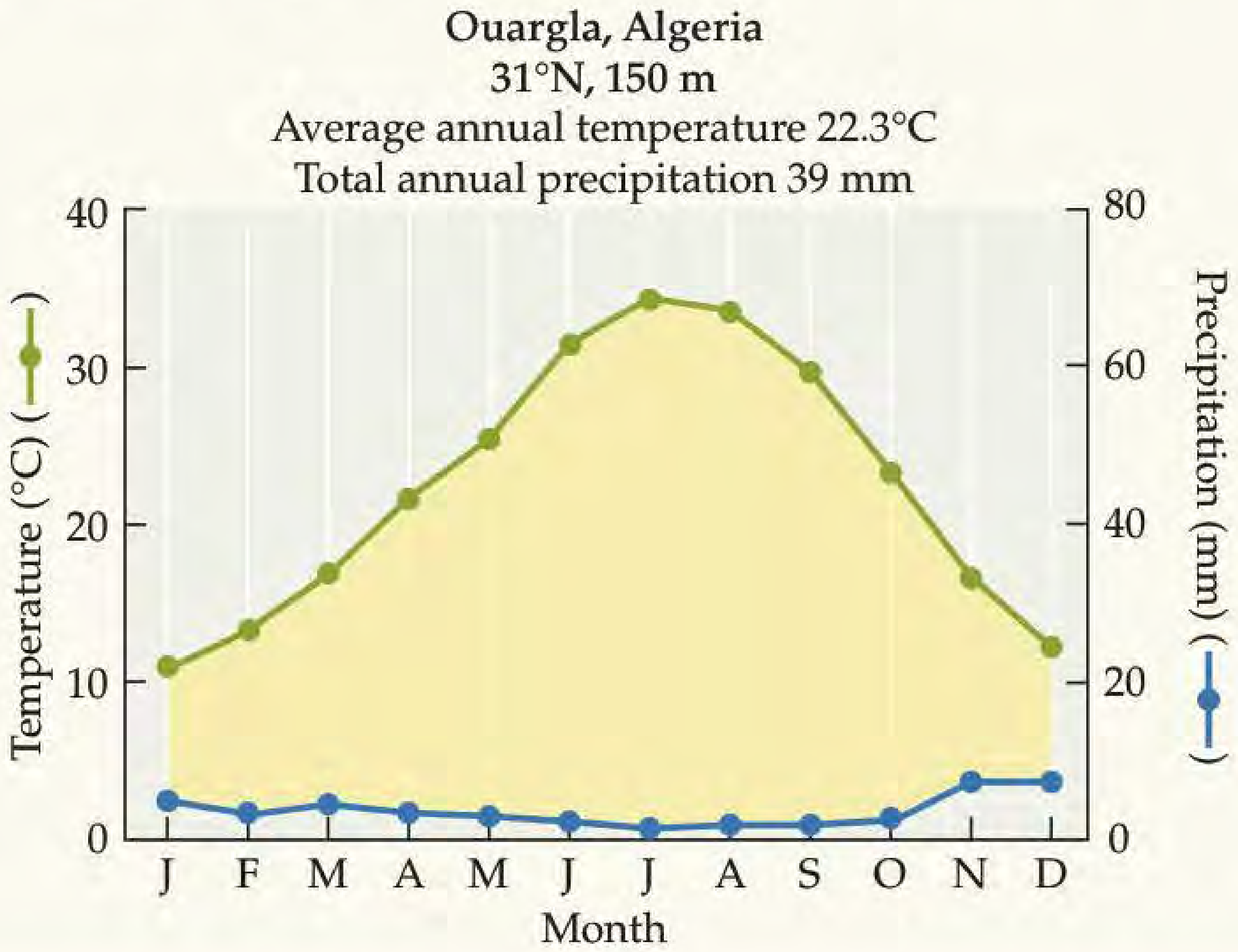
DESERTS



Sand dunes and camelthorn trees (*Acacia erioloba*) in the Namib desert, Namibia, Africa



Sonoran desert in bloom, Organ Pipe National Monument, Arizona, USA



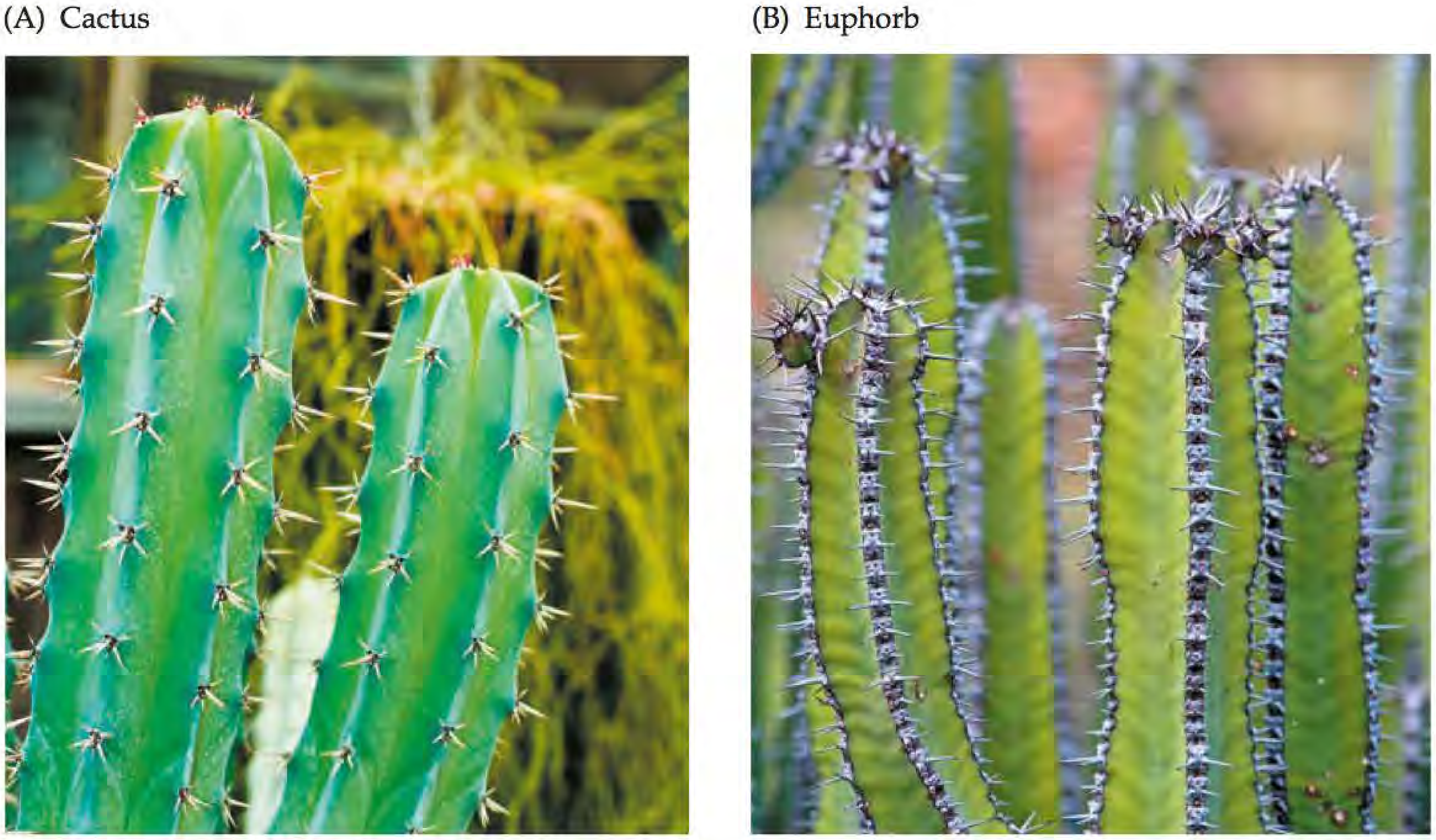


Figure 3.7 Convergence in the Forms of Desert Plants (A) The blue candle cactus (*Myrtillocactus geometrizans*) is native to the Chihuahuan Desert of Mexico. (B) *Euphorbia polyacantha* has cactus-like characteristics. Although only distantly related, both species have succulent stems, water-conserving photosynthetic pathways, upright stems that minimize midday sun exposure, and spines that protect them from herbivores. These traits evolved independently in each species.

sustained periods of high temperatures and low water availability. The subtropical positions of hot deserts correspond with the high pressure zones of the Hadley cells (see Figure 2.8) around 30°N and S, which inhibit the formation of storms and their associated precipitation. Low precipitation levels, coupled with high temperatures and high rates of evapotranspiration, result in a limited supply of water for desert organisms. The major desert zones include the Sahara, the Arabian deserts, the Gobi Desert in Asia, the Atacama Desert of Chile and Peru, and the Chihuahuan, Sonoran, and Mojave Deserts of North America.

Low water availability is an important constraint on the abundance of desert plants as well as an important influence on their form and function. One of the best examples of convergence in plant form is the occurrence of stem succulence in desert plants. Stem succulence occurs in both the cacti of the Western Hemisphere and the euphorb family of the Eastern Hemisphere (**Figure 3.7**). Plants with succulent stems can store water in their tissues to help the plants continue to function during dry periods. Other plants of the desert biome include drought-deciduous shrubs and grasses. Some short-lived annual plants are active only after sufficient precipitation has fallen. These annual plants carry out their entire life cycle, from germination through flowering and seed production, in a few short weeks. Although the abundance of organisms may be low, species diversity can be high in some deserts. The Sonoran Desert, for example, has over 4,500 plant species, 1,200 bee species, and 500 bird species (Nabhan and Holdsworth 1998).

Humans have used deserts for livestock grazing and agriculture for centuries. Agricultural development in desert areas is dependent on irrigation, often using water that flows in from distant mountains or is extracted from deep underground. Unfortunately, irrigated agriculture in deserts has repeatedly failed because of salinization (see Concept 2.6). Livestock grazing in deserts is also a risky venture because of the unpredictable nature of the precipitation needed to support plant growth for herbivores. Long-term droughts in association with unsustainable grazing practices can result in loss of plant cover and soil erosion, a process known as **desertification**. Desertification is a concern in populated regions at the margins of deserts, such as the Sahel region in the southern portion of the Sahara in Africa.

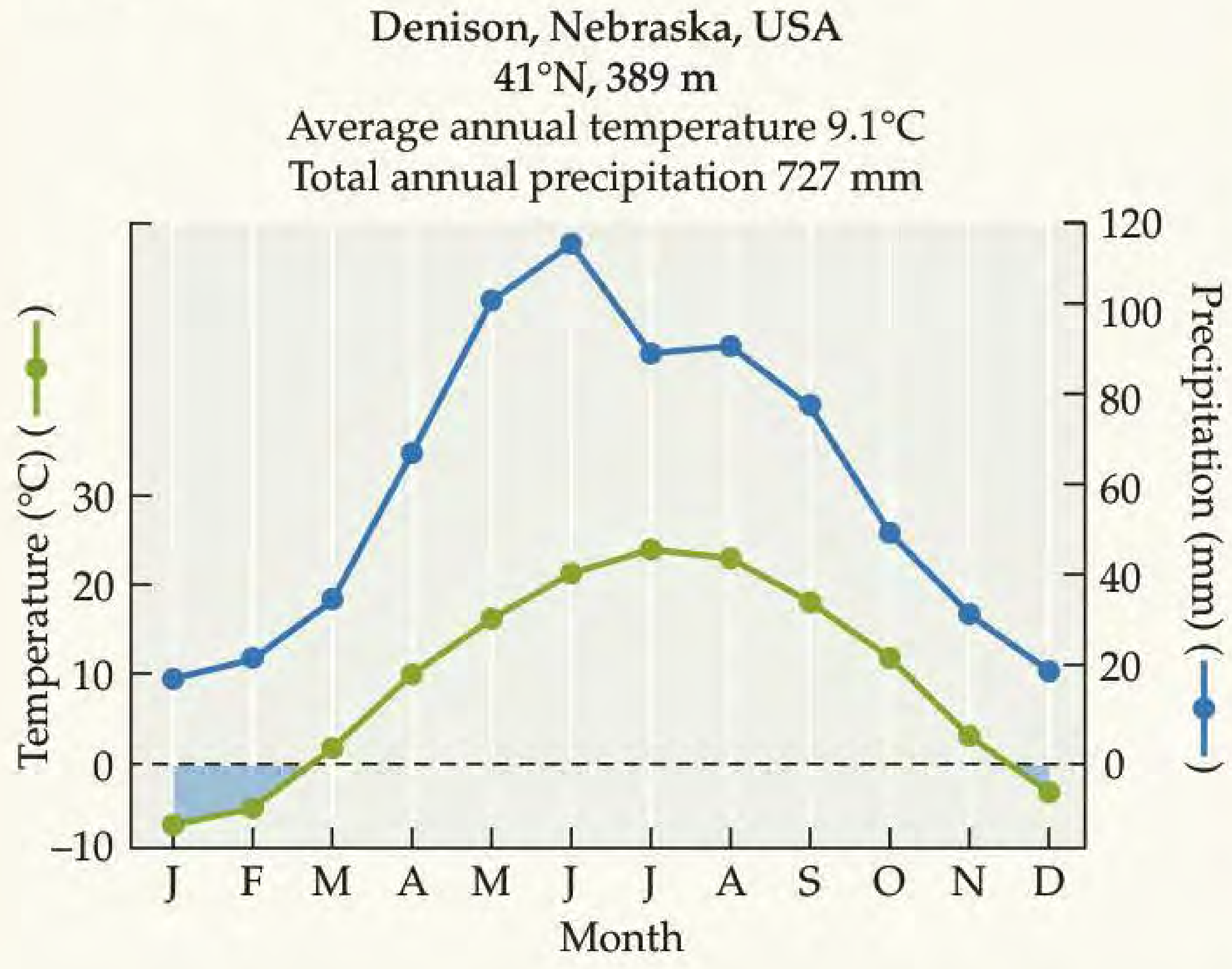
TEMPERATE GRASSLANDS Large expanses of grasslands once occurred throughout North America and Eurasia (the Great Plains and the steppes of Central Asia) at latitudes between 30° and 50°N. Southern Hemisphere grasslands are found at similar latitudes on the east coasts of South America, New Zealand, and Africa. These vast, undulating expanses of grass-dominated landscape have often been compared to a terrestrial ocean, with wind-driven "waves" of plants bending to the gusts blowing through them.

Temperate climates have greater seasonal temperature variation than tropical climates, with increasing periods of subfreezing temperatures toward the poles. Within the temperate zone, grasslands are usually associated with warm, moist summers and cold, dry winters. Precipitation in some grasslands is high enough to support forests, as at the eastern edge of the Great Plains. However, frequent fires and grazing by large herbivores such as bison prevent the establishment of trees and thus maintain the dominance of grasses in these environments. The use of fire to manage grasslands near the edges of forests was probably one of the first human activities with a widespread effect on a terrestrial biome.

The world's grasslands have been a major focus for agricultural and pastoral development. In order to acquire adequate supplies of water and nutrients, grasses grow more roots than stems and leaves. The rich organic matter that accumulates in the soils as a result enhances their fertility, so grassland soils are particularly well suited for agricultural development. Most of the fertile grasslands of central North America and Eurasia have been converted to agriculture. The diversity of the crop species grown on these lands is far less than the diversity of the grasslands they replaced. In more arid grasslands, rates of grazing by domesticated animals can exceed the capacity of the plants to produce new tissues, and grassland degradation, including desertification, may occur. As in deserts, irrigation of some grassland soils has resulted in salinization, decreasing their fertility over time. In parts of Europe, cessation of centuries-old grazing practices has resulted in increased forest invasion into grasslands. This long legacy of use for agriculture and grazing has made grasslands the most human-influenced biome on Earth. You can evaluate the possible effects of climate change in **Analyzing Data 3.1**.

TEMPERATE GRASSLANDS

Sand Hills grasslands at Valentine National Wildlife Refuge, Nebraska, USA



Grassland with chamomile flowers, Altai Plateau, Russia

ANALYZING DATA 3.1 How Will Climate Change Affect the Grasslands Biome?

The climate diagrams shown for each of the terrestrial biomes (pp. 56–68) exemplify the climate patterns with which they are associated (see Ecological Toolkit 3.1). In particular, they show periods of potential plant stress due to low water availability and subfreezing temperatures, which are particularly important in shaping the types of plants that grow in a given location. Global climate change is altering both temperature and precipitation patterns worldwide. Eventually, therefore, the species composition of the biome at a given site will change, as happened following the end of the last Ice Age (see p. 42).

The world's remaining grasslands are particularly threatened by climate change. Much of this biome has already been lost and fragmented by land use change for agricultural and pastoral activities. Current predictions for the tallgrass prairie of the central United States suggest that by 2050, its average annual temperature will increase by 2.3°C and total annual precipitation will not change.

1. Assuming that the changes in temperature occur evenly across the year, draw climate diagrams representing the current and year 2050 conditions for Ellsworth, Kansas, a grassland site in the southern Great Plains. Use the data in the table below for the *current* climate
2. Redraw the climate diagram assuming that winter (December, January, February) precipitation increases by 20% and that summer (June, July, and August) precipitation decreases by 20%, as predicted by some climate change models.
3. Does the diagram from Question 2 show changes in the periods of possible water and temperature stress? If so, how do you think these changes will influence the vegetation composition of the tallgrass prairie? Use the information in Ecological Toolkit 3.1 to assist your reasoning.
4. What factors other than climate should be considered in a prediction of the future fate of the grassland biome?

See the companion website for a similar ANALYZING DATA exercise.

ELLSWORTH, KANSAS, 38°43′ N, 98°14′ W, 466 m ELEVATION

	J	F	M	A	M	J	J	A	S	O	N	D
Average monthly temperature (°C)	−2.1	0.9	6.9	13.1	18.3	23.8	26.9	25.7	20.7	14.3	6.1	−0.2
Average monthly precipitation (mm)	15.2	19.8	56.6	61.5	104.1	102.4	81.8	84.1	79.0	56.1	27.7	19.8

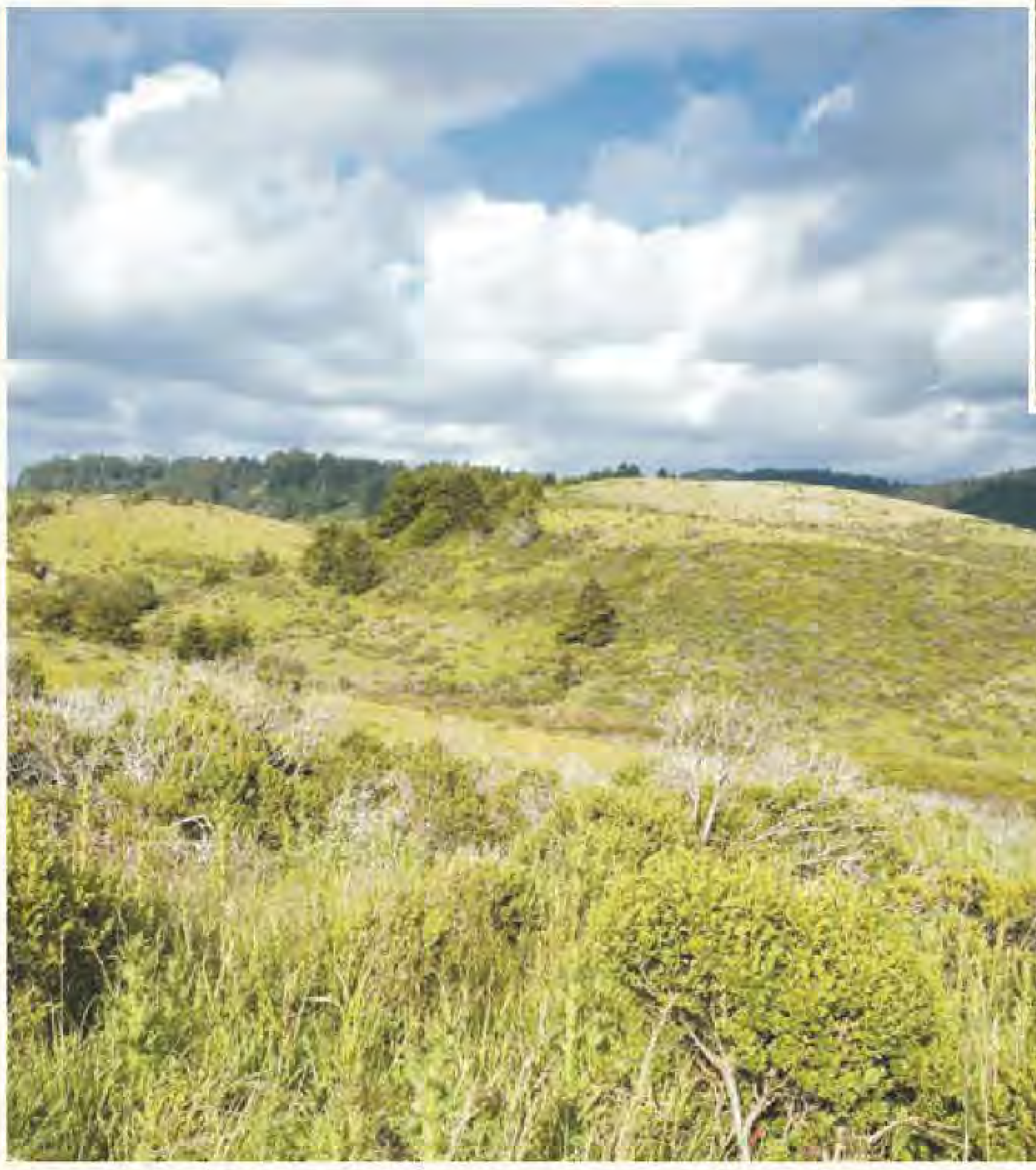
TEMPERATE SHRUBLANDS AND WOODLANDS The seasonality of precipitation is an important control on the distribution of temperate biomes. Woodlands (characterized by an open canopy of short trees) and shrublands occur in regions with a winter rainy season (in contrast to grasslands, with a summer rainy season). *Mediterranean-type climates*, which occur on the west coasts of the Americas, Africa, Australia, and Europe between 30° and 40°N and S, are an example of such a climate regime. As we saw in Concept 2.1, these Mediterranean-type climates are characterized by asynchrony between precipitation and the summer *growing season* (the period of time with suitable temperatures to support growth). Precipitation falls primarily in winter, and hot, dry weather occurs throughout the late spring, summer, and fall. The vegetation of Mediterranean-type climates is characterized by evergreen shrubs and trees. Evergreen leaves allow plants to be active during cooler, wetter periods and also lower their nutrient requirements, since they do not have to develop new leaves every year. Many plants of Mediterranean-type climates have *sclerophyllous* leaves, which are tough, leathery, and stiff. These plants are well adapted to dry soils and may continue to photosynthesize and grow at reduced rates during the hot, dry summer. Sclerophyllous leaves also help to deter consumption by herbivores and prevent wilting as water is lost. Sclerophyllous shrublands are found in each of the zones characterized by a Mediterranean-type climate, including the *mallee* of Australia, the *fynbos* of South Africa, the *matorral* of Chile, the *maquis* around the Mediterranean Sea, and the *chaparral* of North America.

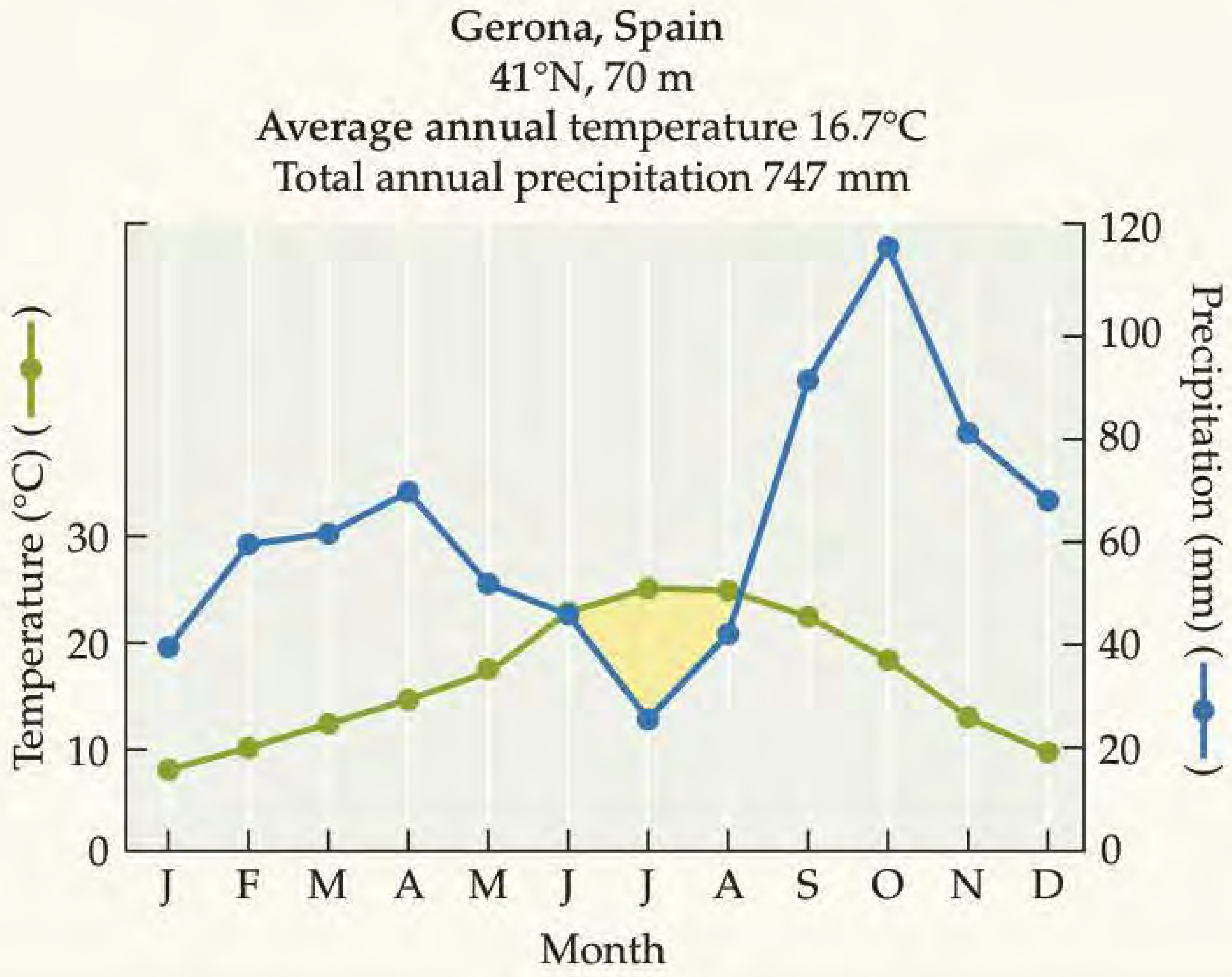
Fire is a common feature in Mediterranean-type shrublands and, as it does in some grasslands, may promote their persistence. Some of the shrubs recover after fires by resprouting from woody storage organs protected from the heat below the ground surface. Other shrubs produce seeds that germinate and grow quickly after a fire. Without regular fires at 30- 40-year intervals, some temperate shrublands may be replaced by forests of oaks, pines, junipers, or eucalypts. Regular disturbance by fire, combined with the unique climate of temperate shrublands, is thought to promote high species diversity.

Shrublands and woodlands are also found in the continental interior of North America and Eurasia, where

TEMPERATE SHRUBLANDS AND WOODLANDS


Fynbos with *Protea* spp. in bloom, Hout Bay Harbour, South Africa


Coastal shrubland in northern California, USA

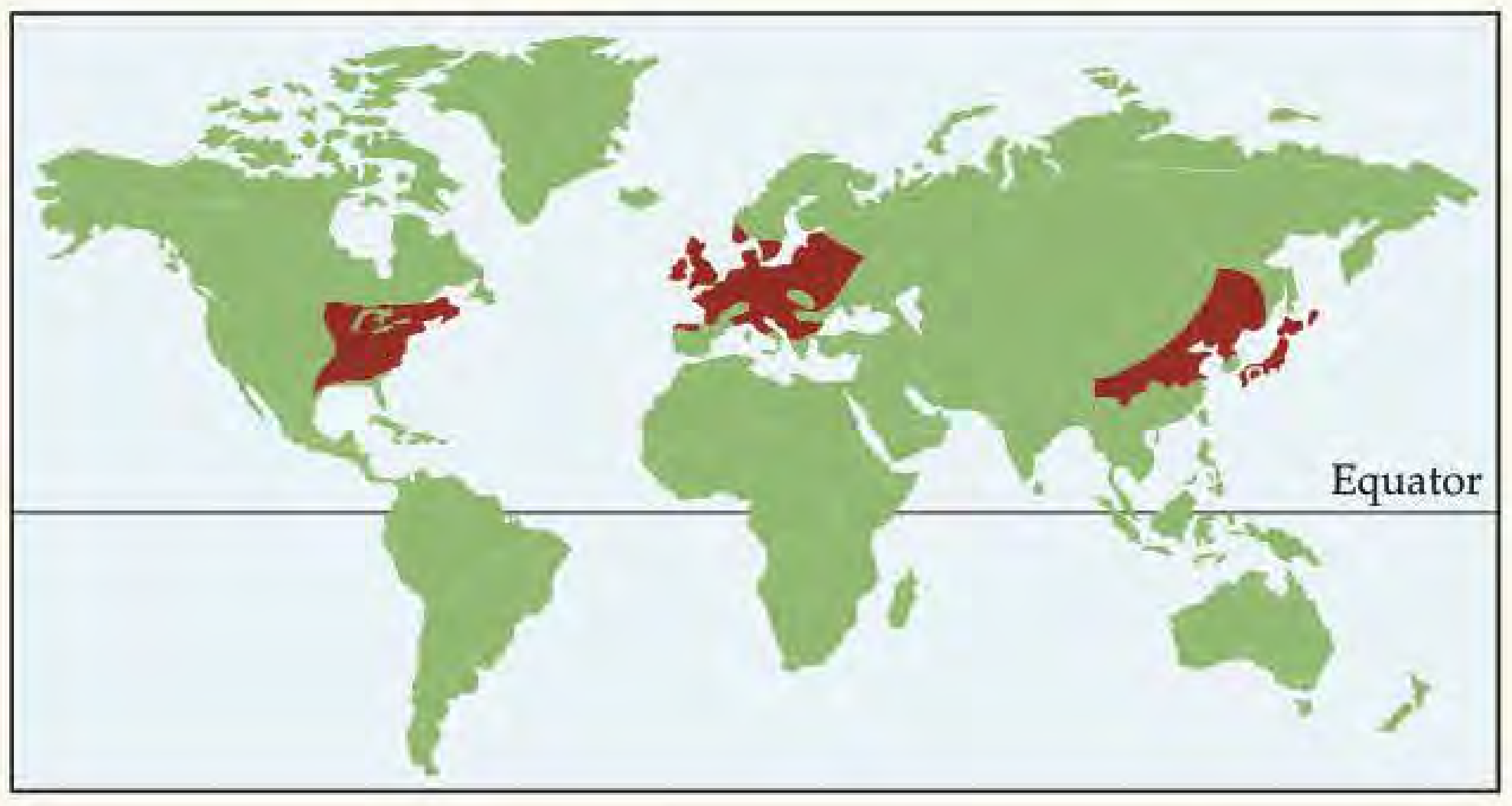


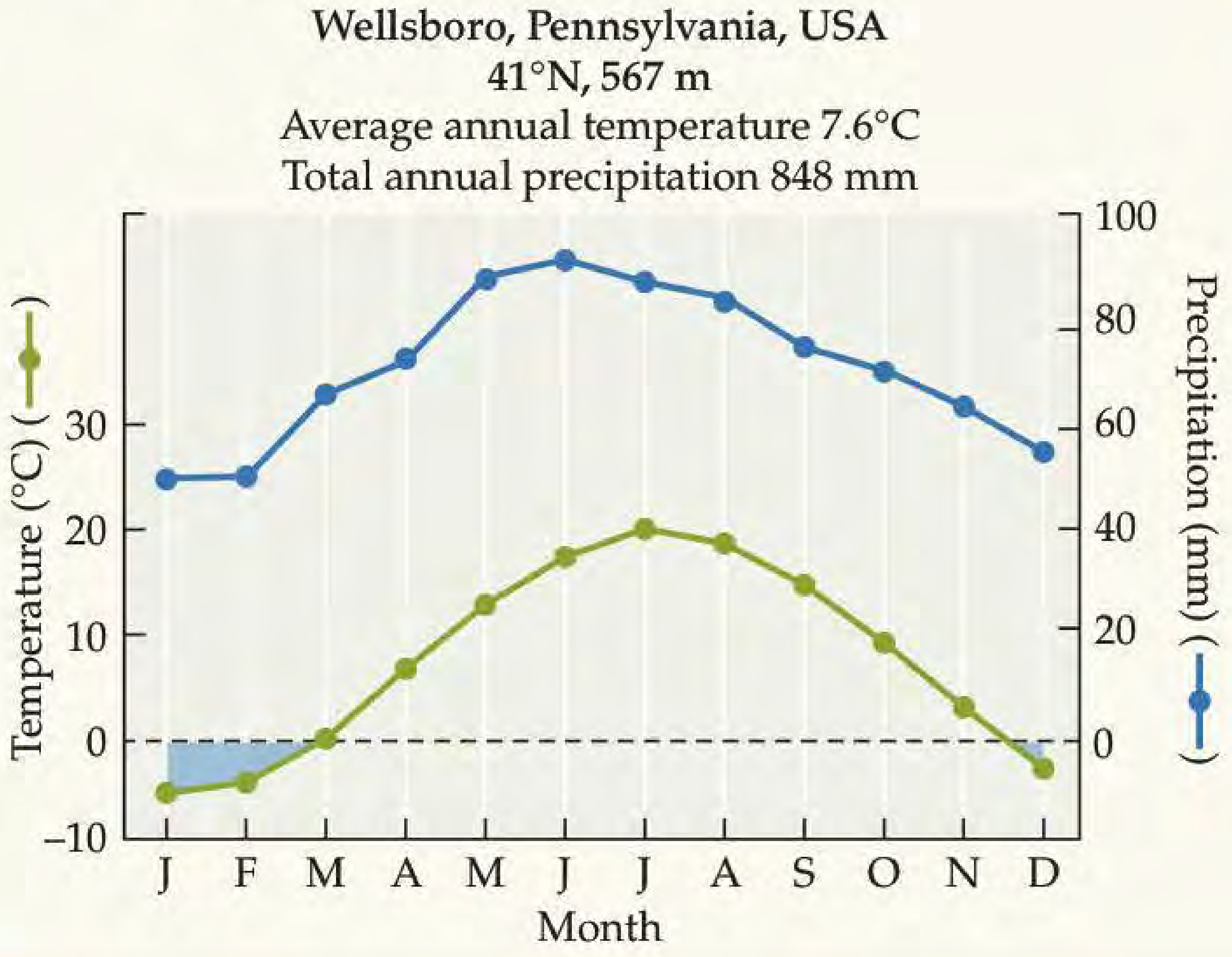
they are associated with rain-shadow effects and seasonally cold climates. The Great Basin, for example, occupies the interior of North America between the Sierra Nevada and the Cascade Range to the west and the Rocky Mountains to the east. Large expanses of sagebrush (*Artemisia tridentata*), saltbush (*Atriplex* spp.), creosote bush (*Larrea tridentata*), and piñon pine and juniper woodland occur throughout this area.

Humans have converted some regions of temperate shrublands and woodlands to croplands and vineyards. However their climates and nutrient-poor soils have limited the extent of agricultural and pastoral development. In the Mediterranean basin, agricultural development using irrigation was attempted but failed because of the infertile soils. Urban development has reduced the cover of shrublands in some regions (e.g., Southern California). Increases in local human populations have increased the frequency of fires, which has decreased the ability of shrubs to recover and may lead to their replacement by invasive annual grasses.

TEMPERATE DECIDUOUS FORESTS

Autumn foliage prior to leaf fall, Great Smoky Mountains National Park, North Carolina, USA





Beech forest in summer, Japan

TEMPERATE DECIDUOUS FORESTS Deciduous leaves are a solution to the extended periods of freezing weather in the temperate zone. Leaves are more sensitive to freezing than other plant tissues because of the high level of physiological activity associated with photosynthesis. Temperate deciduous forests occur in areas where there is enough rainfall to support tree growth (500–2,500 mm, or 20–100 inches, per year) and where soils are fertile enough to supply the nutrients lost when leaves are shed in the fall. Temperate deciduous forests are primarily limited to the Northern Hemisphere, as the Southern Hemisphere contains less land area and lacks extensive areas with the continental climates associated with the deciduous forest biome.

Deciduous forests occur at 30° to 50°N on the eastern and western edges of Eurasia and in eastern North America, extending inland to the continental interior before diminishing because of lack of rainfall and, in some cases, increased fire frequency. Similar species occur on each of these continents, reflecting a common biogeographic history (see Chapter 18). Oak, maple, and beech trees, for example, are components of this forest biome on each continent. The vertical structure of the forest includes canopy trees as well as shorter trees, shrubs, and forbs below the canopy. Species diversity is lower than in tropical forests but can be as high as 3,000 plant species (e.g., in eastern North America). Disturbances such as fire and outbreaks of herbivorous insects do not play a major role in determining the development and persistence of temperate deciduous forest vegetation, although they can influence its boundaries, and periodic outbreaks of herbivores (e.g., the gypsy moth, a non-native insect introduced to North America) do occur.

The temperate deciduous forest biome has been a focus for agricultural development for centuries. The fertile soils and climate are conducive to the growth of crops. Forest clearing for crop and wood production has historically been widespread in this biome. Very little old-growth temperate deciduous forest remains on any continent. Since the early twentieth century, however, agriculture has gradually shifted away from temperate-zone forests toward temperate grasslands and the tropics, particularly in the Americas. Abandonment of agricultural fields has resulted in reforestation in some parts of Europe and North America. However, the species composition of the second-growth forests often differs from what was present prior to agricultural development. Nutrient loss from soils due to long-term agricultural use is one reason for this difference. Another is the loss of some species due to introductions of invasive species. For example, the chestnut blight fungus, introduced from Asia, nearly wiped out the chestnut trees (*Castanea* spp.) of North America in the early twentieth century (see Figure 13.14). As a result, oak species are more widespread than they were prior to agricultural development.

TEMPERATE EVERGREEN FORESTS Evergreen forests span a wide range of environmental conditions in the temperate zone, from warm coastal zones to cool continental and maritime climates. Precipitation also varies substantially among these forests, from 500 to 4,000 mm (20–150 inches) per year. Some temperate evergreen forests with high levels of precipitation, which are typically located on west coasts at latitudes between 45° and 50°N and S, are referred to as "temperate rainforests" (**Figure 3.8**). Temperate evergreen forests are commonly found on nutrient-poor soils, whose condition is in part related to the acidic nature of the leaves of the evergreen trees. Some evergreen forests are subject to regular fires at intervals of 30–200 years, which may promote their persistence.

Temperate evergreen forests are found in both the Northern and Southern Hemispheres between 30° and 50° latitude. Their diversity is generally lower than that of deciduous and tropical forests. In the Northern Hemisphere, the tree species include needle-leaved conifers such as pines, junipers, and Douglas fir (*Pseudotsuga menziesii*). In the Southern Hemisphere, on the west coasts of Chile and Tasmania, in southeastern and southwestern Australia, and in New Zealand, there is a greater diversity of tree species, including southern beeches (*Nothofagus* spp.), eucalypts, the Chilean cedar (*Austrocedrus*), and podocarps (see Figure 18.4).

Conifers provide a source of high-quality wood and pulp for paper production. The temperate evergreen forest biome has been subjected to extensive clearing, and little old-growth forest remains. Some forestry practices tend to promote sustainable use of these forests, although in some regions the planting of non-native species (such as Monterey pine in New Zealand), the uniform age and density of the trees, and losses of formerly dominant species have created forests that are ecologically very different from their pre-logging condition. The suppression of naturally occurring fires in western North America has increased the density of some forest stands, which has resulted in more intense fires when they do occur and has increased the spread of insect pests (e.g.,

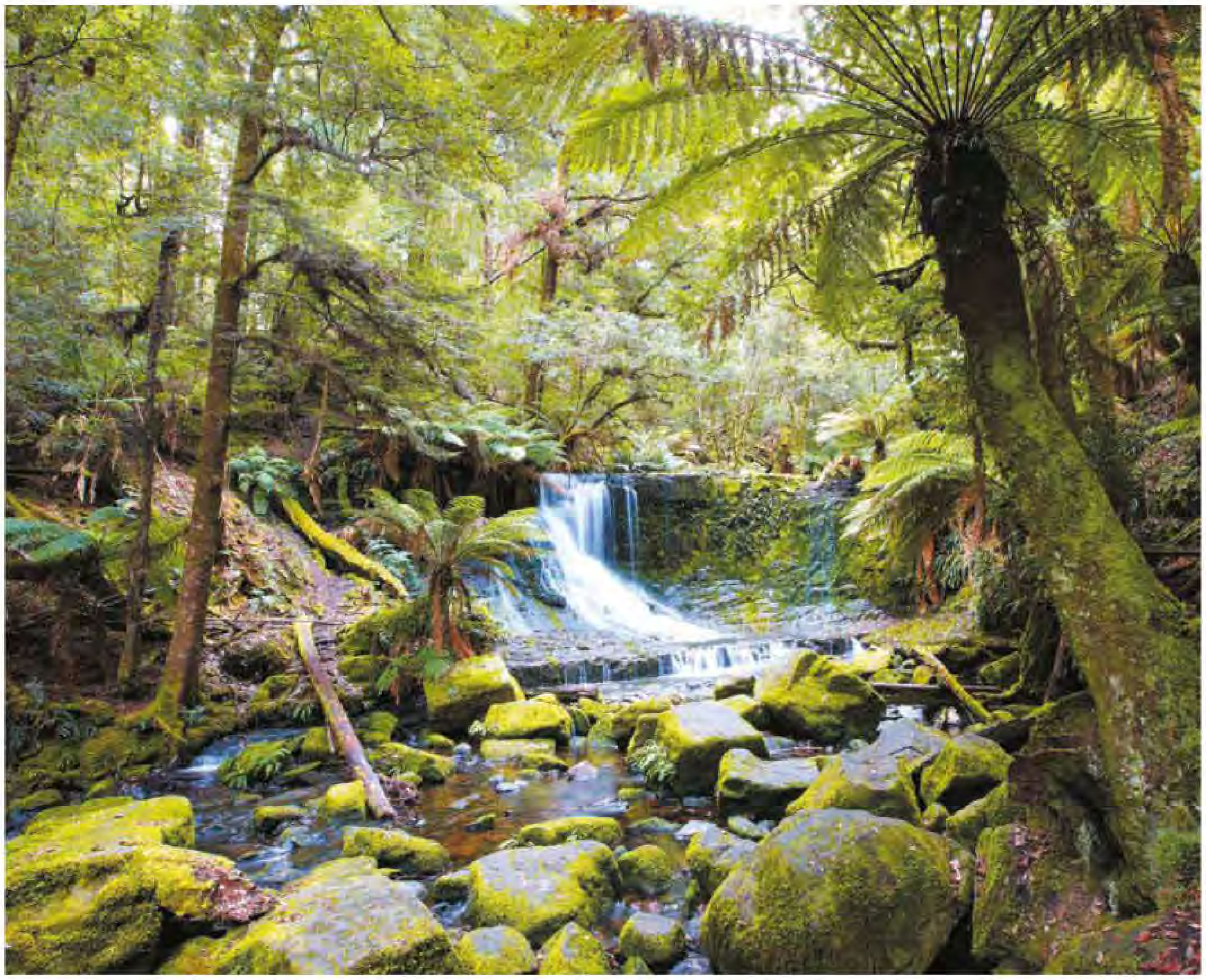
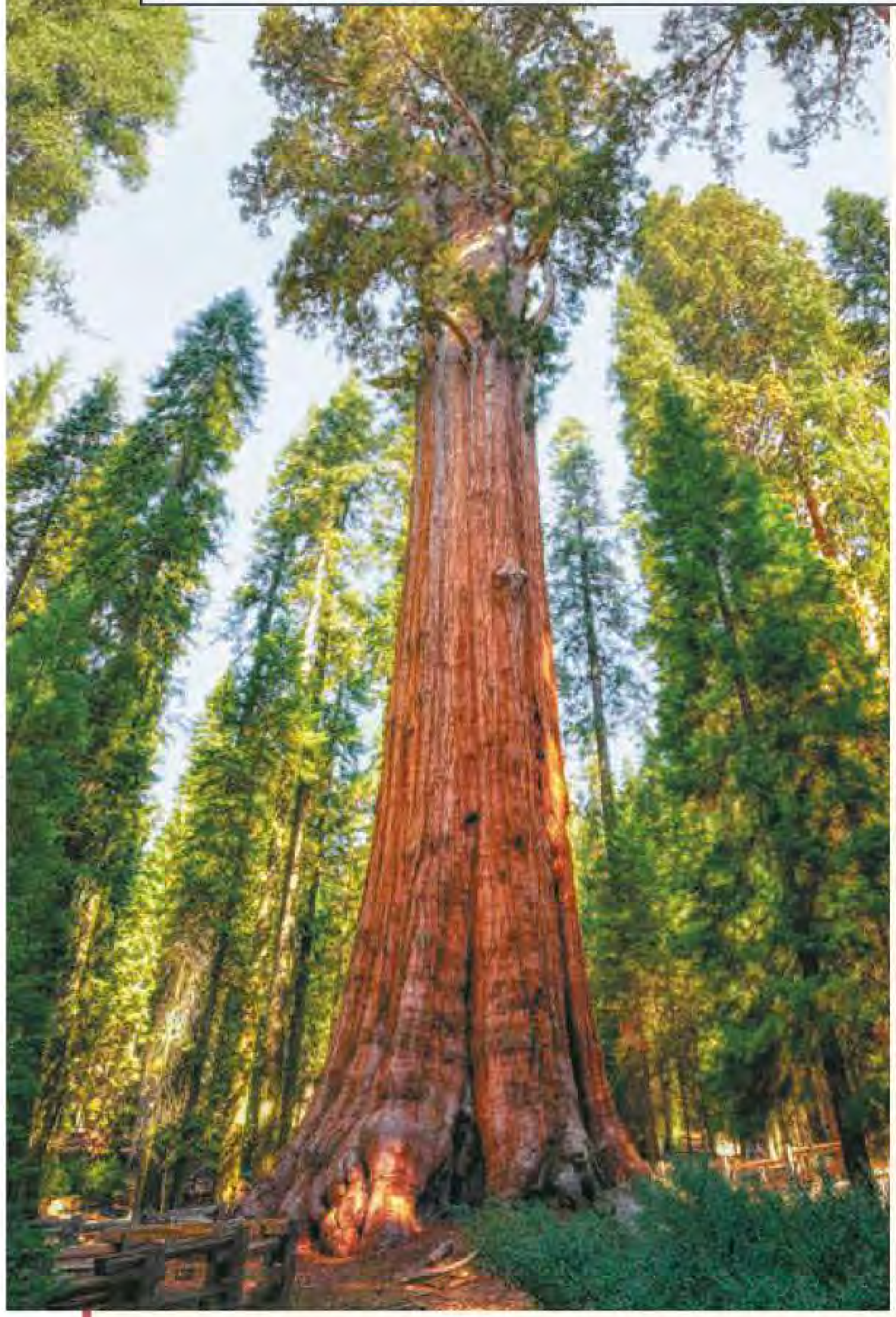


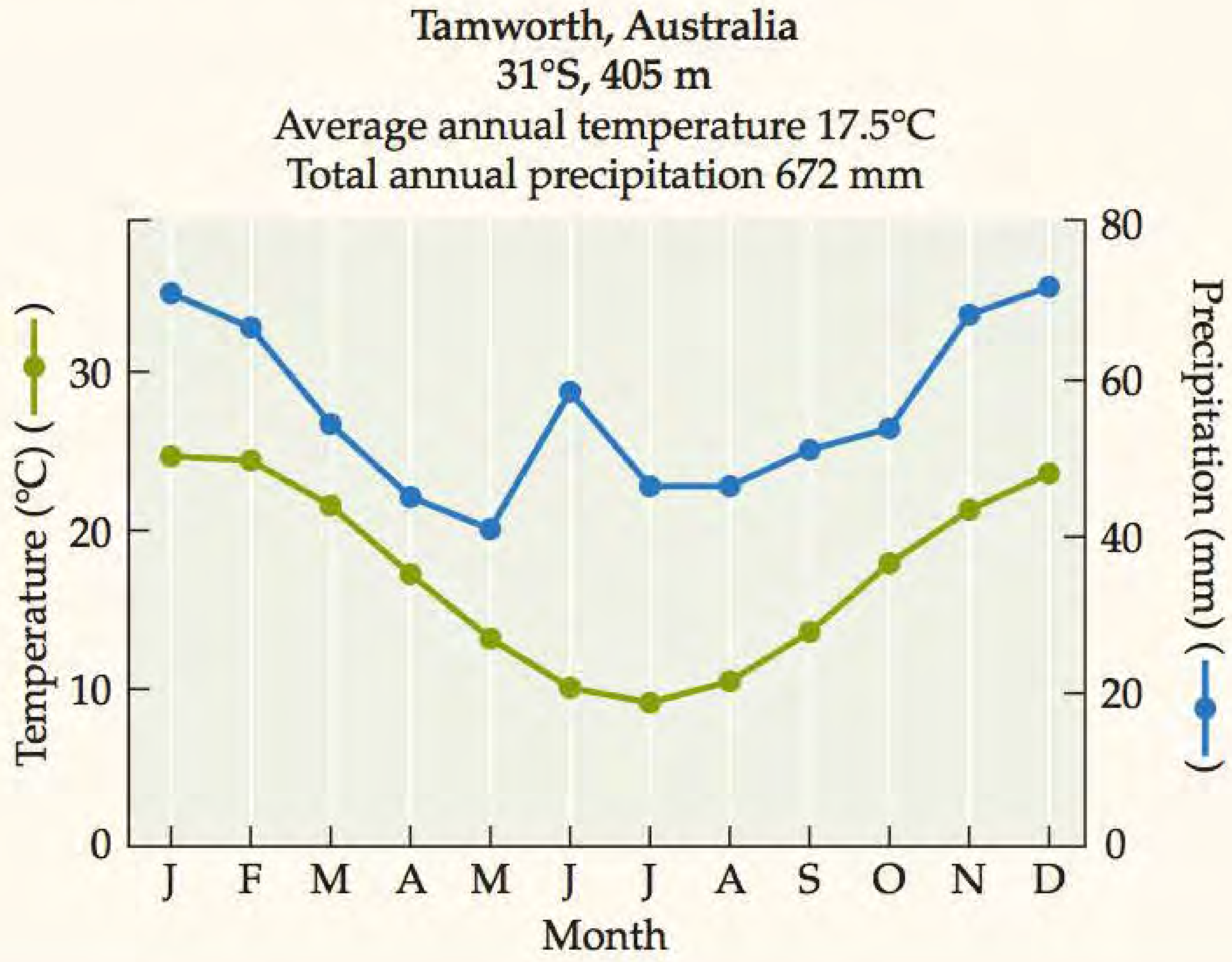
Figure 3.8 Temperate Rainforest Rainforests occur in temperate zones with high precipitation (over 5,000 mm, or 200 inches) and relatively mild winter temperatures. Here, understory tree ferns grow beneath the canopy trees at Horseshoe Falls in western Tasmania, Australia.

TEMPERATE EVERGREEN FORESTS



Grove of giant sequoias (*Sequoiadendron giganteum*), Sequoia National Park, California, USA

Araucaria (monkey puzzle tree) forest, Lanin National Park, Argentina



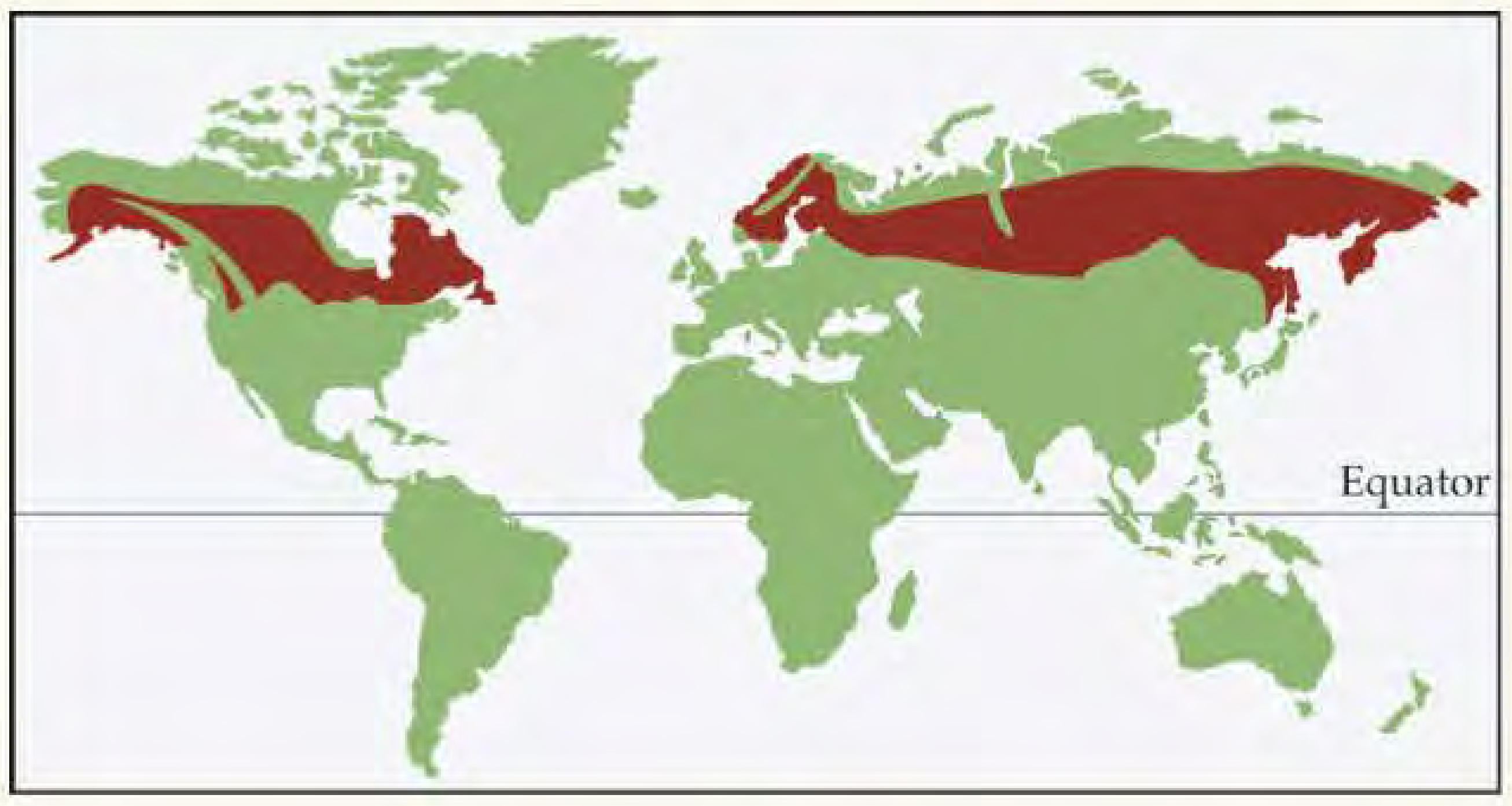
bark beetles) and pathogens. In industrialized countries, the effects of air pollution have damaged some temperate evergreen forests (see Figure 25.18) and made them more susceptible to other stresses.

BOREAL FORESTS Above 50°N, the severity of winters increases. Minimum temperatures of –50°C (–58°F) are common in continental locations such as Siberia, and continuous subfreezing temperatures may last up to 6 months. The extreme weather in these subarctic regions is an important determinant of the vegetation structure. Not only must the plants cope with low air temperatures, but soils may regularly freeze, leading to the formation of **permafrost**, defined as a subsurface soil layer that remains frozen year-round for at least 3 years. Although precipitation is low, the permafrost impedes water drainage, so soils are moist to saturated.

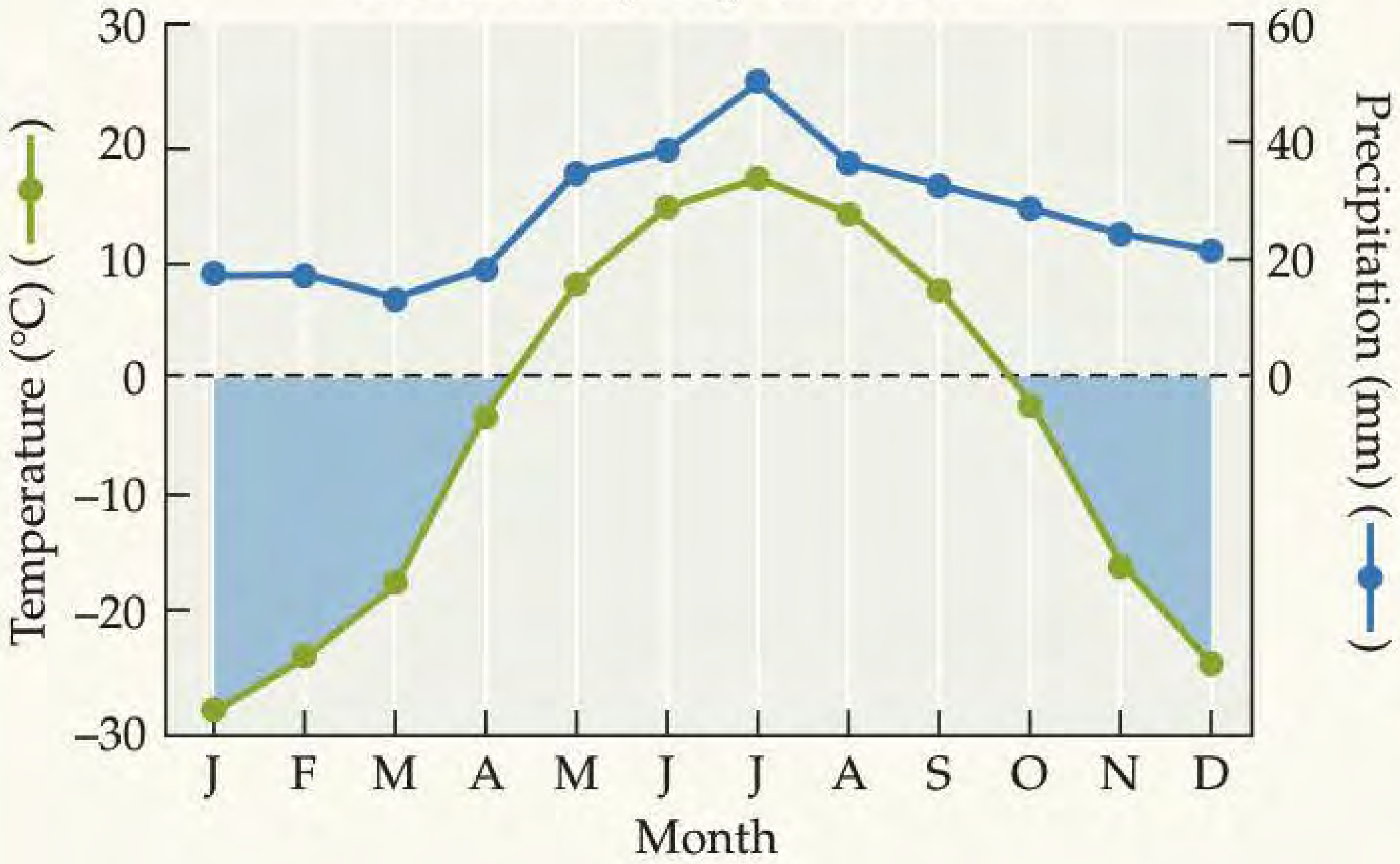
The biome that occupies the zone between 50° and 65°N is the boreal (far northern) forest. This biome is also known as *taiga*, the Russian word for this northern forest. It is composed primarily of coniferous species, including spruces, pines, and larches (deciduous needle-leaved trees) but also includes extensive deciduous birch forests in maritime locations, particularly in Scandinavia. Conifers tend to resist damage from winter freezing better than angiosperm trees, despite

BOREAL FORESTS

Boreal forest in autumn, Denali National Park, Alaska, USA



Fort Simpson, Northwest Territories, Canada
61°N, 169 m
Average annual temperature –4.6°C
Total annual precipitation 333 mm



Spruce (*Picea abies*) and silver birch (*Betula verrucosa*) along the Kitkajoki River, Oulanka National Park, Finland

maintaining green leaves year-round. Although the boreal forest is found only in the Northern Hemisphere, it is the largest biome in area and contains one-third of Earth's forested land.

Boreal forest soils are cold and wet, limiting the decomposition of plant material such as leaves, wood, and roots. Thus, the rate of plant growth exceeds the rate of decomposition, and the soils contain large amounts of organic matter. During extensive summer droughts, forests are more susceptible to fires ignited by lightning. These fires may burn both the trees and the soil (**Figure 3.9**). Soil fires may continue to burn slowly for several years, even through

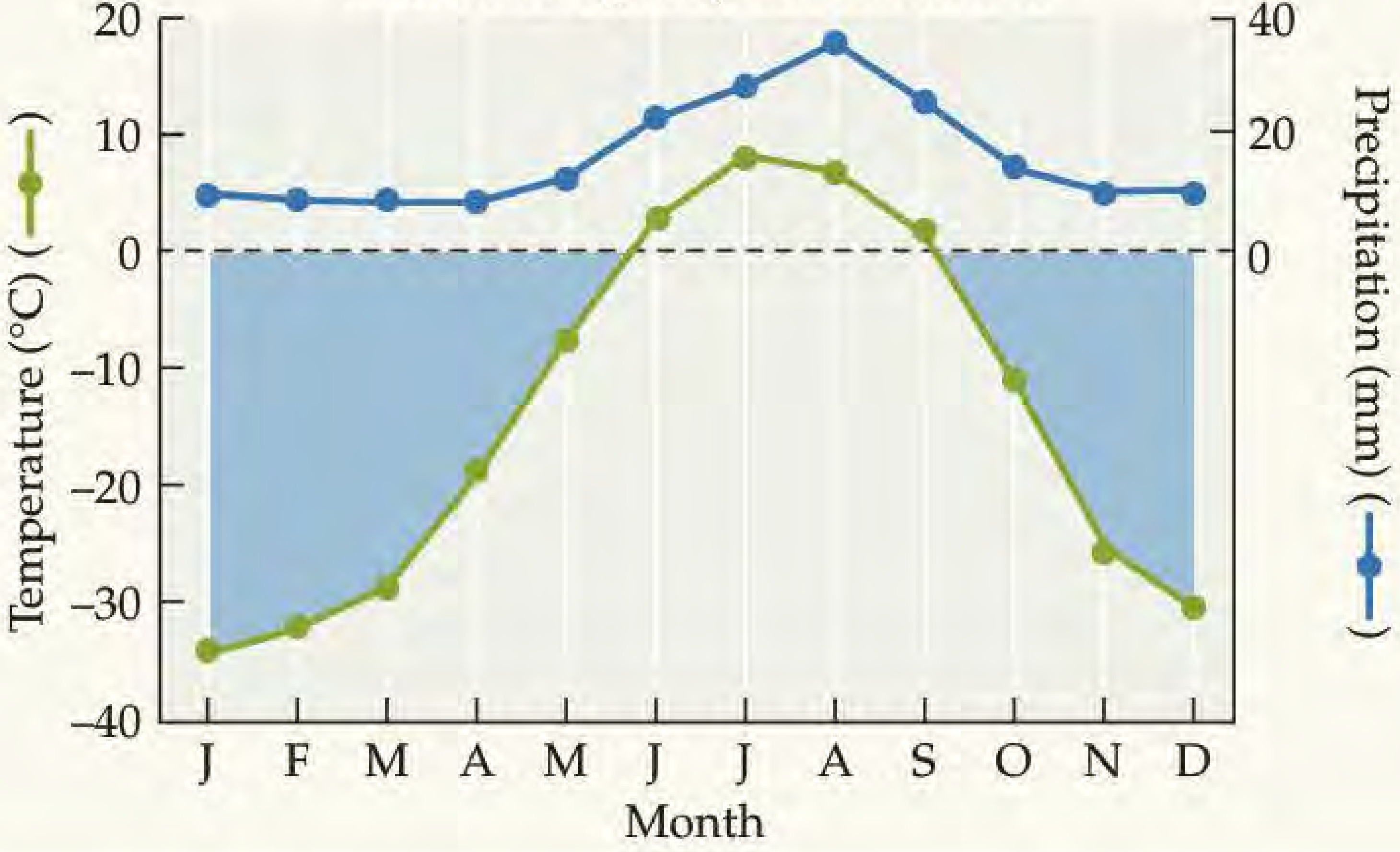
Figure 3.9 Fire in the Boreal Forest Despite the cold climate of the boreal forest, fire is an important part of its environment.

TUNDRA

Arctic tundra in early autumn color, Skeidararjokull glacier, Iceland

Dwarf shrubs and shrubby willows in Arctic tundra below Denali National Park in interior Alaska

Olenek, Russia
73°N, 11 m
Average annual temperature –14.3°C
Total annual precipitation 184 mm



the cold winters. In the absence of fire, forest growth enhances permafrost formation by lowering the amount of sunlight absorbed by the soil surface. In low-lying areas, soils become saturated, killing the trees and forming extensive peat bogs.

Boreal forests have been less affected by human activities than other forest biomes. Logging occurs in some regions, as does oil and gas development, including the mining of oil sands. These activities will pose an increasing threat to the boreal forest as demands for wood and energy increase. In addition, the large store of organic matter in the soil makes boreal forests an important component of the global carbon cycle. Climate warming may result in more rapid decomposition and thus higher rates of carbon release from boreal forest soils, increasing atmospheric greenhouse gas concentrations that in turn cause additional warming (see Concept 25.2).

TUNDRA Trees cease to be the dominant vegetation beyond approximately 65° latitude. The tree line that marks the transition from boreal forest to tundra is associated with low growing-season temperatures, although the causes of this transition are complex and can also include other climate and soil conditions. The tundra biome occurs primarily in the Arctic but can also be found on the edges of the Antarctic Peninsula and on a few islands in the Southern Ocean. The poleward decrease in temperature and precipitation across the tundra biome is associated with the zones of high pressure generated by the polar atmospheric circulation cells (see Figure 2.8).

The tundra biome is characterized by sedges, forbs, grasses, and low-growing shrubs such as heaths, willows, and birches. Lichens and mosses are also important components of this biome. Although the summer growing season is short, the days are long, with continuous periods of light for 1 to 2 months of the summer. The plants and lichens survive the long winter by going dormant, maintaining living tissues under the snow or soil, where they are insulated from the cold air temperatures.

The tundra and the boreal forest have several similarities: temperatures are cold, precipitation is low, and permafrost is widespread. Despite the low precipitation, many tundra areas are wet, as the permafrost keeps the precipitation that does fall from percolating to deeper soil layers. Repeated freezing and thawing of surface soil layers over several decades results in sorting of soil materials according to their texture. This process forms polygons of soil at the surface with upraised rims and depressed centers (**Figure 3.10**). Where soils are coarser or permafrost does not develop, the soils may be dry, and plants must be able to cope with low water availability. These polar deserts are most common at the high latitude limit of the tundra biome.

Herds of caribou and musk oxen, as well as predators such as wolves and brown bears, inhabit the tundra. Many species of migratory birds nest in the tundra during the summer. Human inhabitants are scattered in sparse settlements. As a result, this biome contains some of the largest pristine regions on Earth. The influence of human activities on the tundra is increasing, however. Exploration and development of energy resources has accelerated. A key to limiting the effects of energy development is preventing damage to the permafrost, which can cause long-term erosion. The Arctic has experienced climate warming almost double the global average during the late twentieth and early twenty-first centuries. Increased losses of permafrost, catastrophic lake drainage, and reduced carbon storage in the soil have been linked to climate change.

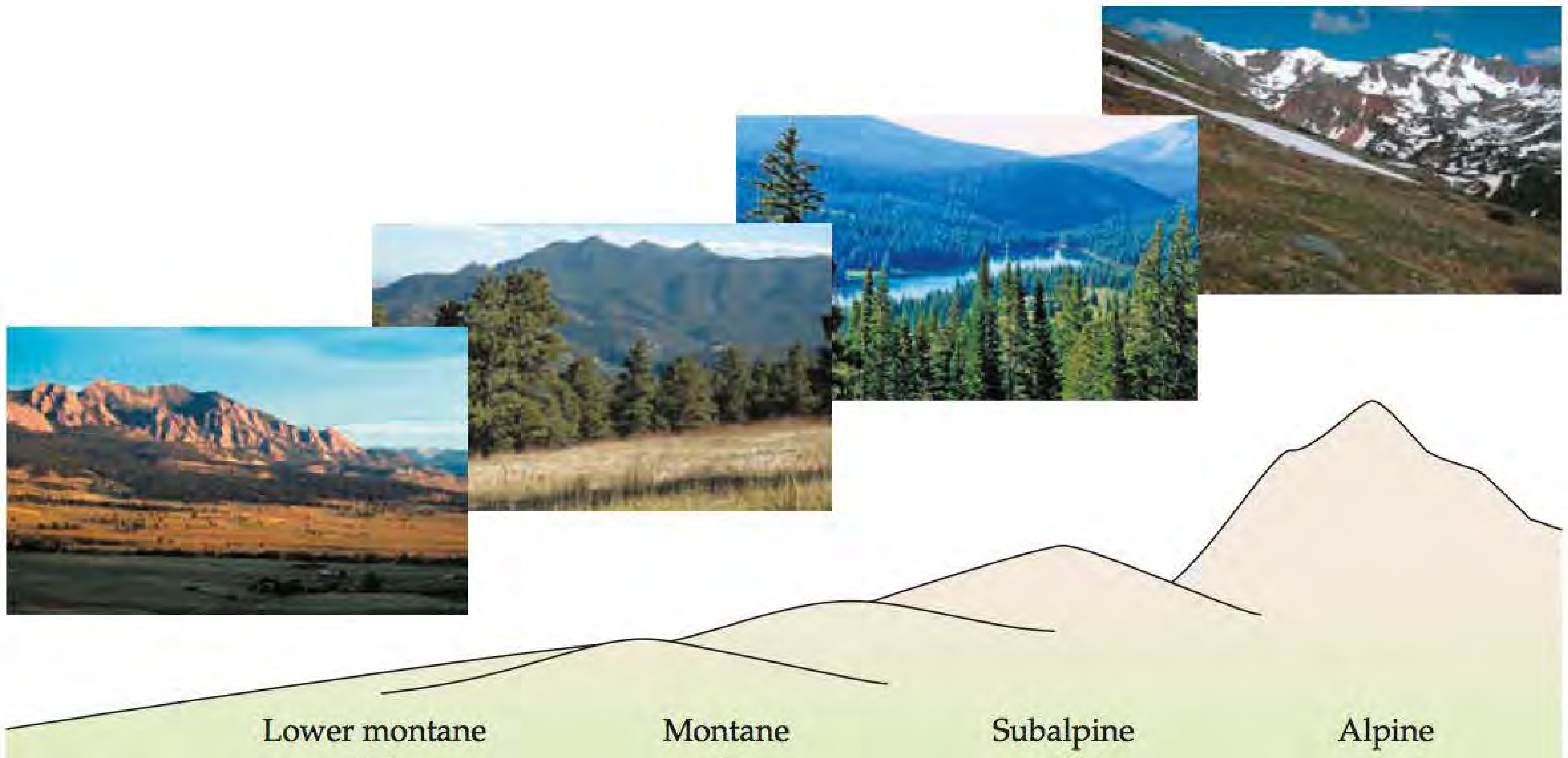
Figure 3.10 Soil Polygons and Pingo Pingos are small hills found in the Arctic, formed by an intrusion of water that freezes in the subsurface permafrost zone, thrusting the soil above it upward. The polygons on the periphery of the pingo result from freezing and thawing of soils, a process that pushes coarse soil materials toward the edges and finer soil to the middle of the polygons.

Now that we've completed our tropics-to-tundra tour of terrestrial biomes, let's consider the influence of mountains on more local-scale patterning of biological communities. In some mountainous locations, elevational changes result in a smaller version of our latitudinal description of biomes.

Biological communities in mountains occur in elevational bands

Approximately one-fourth of Earth's land surface is mountainous. Mountains create climate gradients that change more rapidly over a given distance than those associated with changes in latitude. Temperatures decrease with elevation (for reasons described in Concept 2.3); for example, temperatures in temperate continental mountain ranges decrease approximately 6.4°C for every 1,000 m increase in elevation (or 3.6°F per 1,000 feet), a decrease equivalent to that over approximately a 13° change in latitude, or a distance of 1,400 km (870 miles). As we might expect from our consideration of biomes and their close association with climate, coarse biotic assemblages similar to biomes occur in elevational bands on mountains. Finer-scale biotic distinctions are found in association with slope aspect (e.g., north-facing versus south-facing), proximity to streams, and the orientation of slopes in relation to prevailing winds (see Concept 2.4).

The biological communities that occur from the base to the summit of a temperate-zone mountain range resemble what we would find along a latitudinal gradient toward higher latitudes. An elevational transect on the eastern slope of the southern Rocky Mountains in Colorado, for example, includes grassland to alpine vegetation across a 2,200 m (7,200-foot) increase in elevation (**Figure 3.11**). The changes in climate and vegetation are similar to the transition from grassland to tundra that occurs with a 27° increase in latitude, from Colorado to the Northwest Territories of Canada. Grasslands occur at the base of the mountains, but they give way to pine savannas on the initial slopes (the lower montane zone). Fire plays an important role in determining the vegetation structure of both montane grasslands and savannas. With increasing elevation, the pine savannas are replaced by denser stands of mixed pine–aspen forests (the montane zone), which resemble temperate evergreen and deciduous forest biomes. Spruce and fir trees make up the forests of the subalpine zone, which resemble the boreal forest biome. Mountain tree lines are similar to the transition from boreal forest to tundra, although topography can play an important role through its influence on snow distribution



	Lower montane zone	Montane zone	Subalpine zone	Alpine zone
Median elevation (m)	1,500	2,400	3,000	3,700
Mean annual temperature (°C)	9	5.5	2.5	–3.5
Mean annual precipitation (mm)	450	600	750	1,000

Figure 3.11 Mountain Biological Zones An elevational transect on the eastern slope of the southern Rocky Mountains passes through climate conditions and biome-like assemblages similar to those found along a latitudinal gradient between Colorado and northern Canada. (Data from Marr 1967.)

? Would you expect the same biological zonation on east-facing and west-facing slopes in a temperate mountain range near the west coast of a continent?

and avalanches. The alpine zone above the tree line includes diminutive plants such as sedges, grasses, and forbs, including some of the same species that occur in the Arctic tundra. Although the alpine zone resembles the tundra, its physical environment is different, with higher wind speeds, more intense solar radiation, and lower atmospheric partial pressures of O_2 and CO_2.[1]

Mountains are found on all continents and at all latitudes. As indicated in the example above, the changes in climate associated with changes in elevation alter the composition of the local vegetation. Not all of the vegetation assemblages that occur in mountains resemble major terrestrial biomes, however. Some mountain-influenced biological communities have no biome analogs. For example, daily temperature changes at high-elevation sites in the tropics (e.g., Mount Kilimanjaro and the tropical Andes) are greater than seasonal temperature changes. Subfreezing temperatures occur on most nights in the tropical alpine zone. As a result of these unique climate conditions, tropical alpine vegetation does not resemble that of the temperate alpine zone or the Arctic tundra (**Figure 3.12**).

Figure 3.12 Tropical Alpine Plants Frailejón (*Espeletia* spp.) grows in alpine grasslands in the Ecuadorian Andes. Its growth form, characterized by a circle of leaves (rosette), is typical of plants in the tropical alpine zones of South America and Africa. The adult leaves help protect the developing leaves and stems at the apex of the plant from nightly frosts. Such giant rosettes are found exclusively in the tropical alpine zone and do not have analogs in the Arctic or Antarctic.

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[1] The *partial pressure* of a gas is defined as the pressure exerted by a particular component of a mixture of gases. The concentrations of CO_2 and O_2 are the same at high elevations as they are at sea level, but their partial pressures are lower because total atmospheric pressure is lower. The exchange of a gas between an organism and the atmosphere is determined by its partial pressure rather than its concentration.

CONCEPT 3.2

Biological zones in freshwater ecosystems are associated with the velocity, depth, temperature, clarity, and chemistry of the water.

Freshwater Biological Zones

Although they occupy a small portion of the terrestrial surface, freshwater streams, rivers, and lakes are a key component in the connection between terrestrial and marine ecosystems. Rivers and lakes process inputs of chemical elements from terrestrial ecosystems and transport them to the oceans. The biota of these freshwater ecosystems reflect the physical characteristics of the water, including its velocity (flowing streams and rivers versus lakes and ponds), its temperature (including seasonal changes), how far light can penetrate it (clarity), and its chemistry (salinity, oxygen concentrations, nutrient status, and pH).

In this section we will explore the biota and associated physical conditions found in freshwater ecosystems. In contrast to terrestrial biomes, for which only plants are used as indicators, the biological assemblages of freshwater ecosystems are characterized by both plants and animals, reflecting the greater proportional abundance of animals in aquatic ecosystems.

Biological communities in streams and rivers vary with stream size and location within the stream channel

Water flows downhill over the land surface in response to the force of gravity. The land surface is partly shaped by the erosional power of water, which cuts valleys as it heads toward a lake or ocean. The descending water converges into progressively larger streams and rivers, called **lotic** (flowing water) ecosystems. The smallest streams at the highest elevations in a landscape are called *first-order streams* (**Figure 3.13**). Two first-order streams may converge to form a second-order stream. Large rivers such as the Nile or Mississippi are equal to or greater than sixth-order streams.

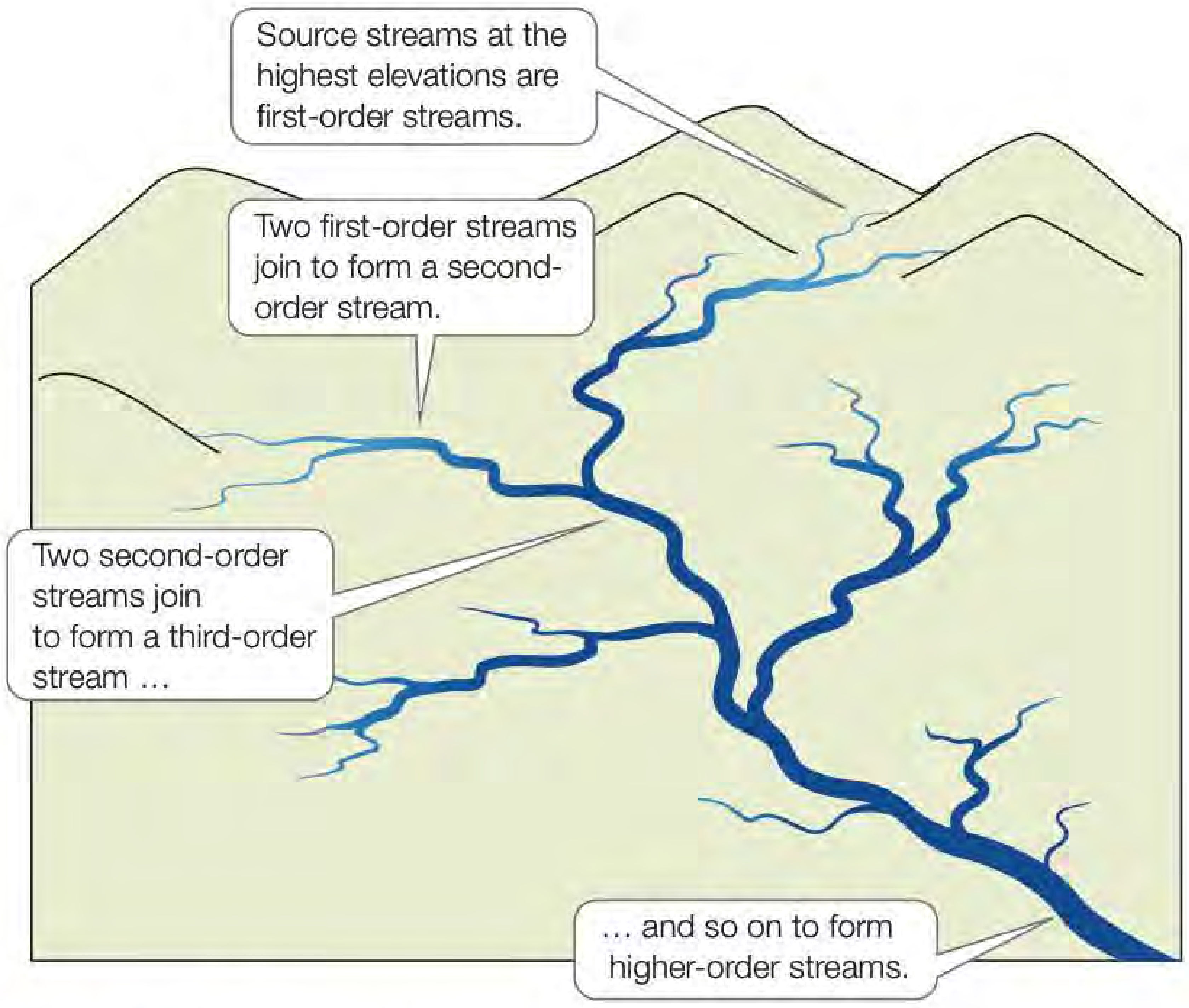


Figure 3.13 Stream Orders Stream order affects environmental conditions, community composition, and the energy and nutrient relationships of communities within the stream.

Individual streams tend to form repeated patterns of riffles and pools along their paths. *Riffles* are fast-moving portions of the stream flowing over coarse particles on the stream bed, which increase oxygen input into the water. *Pools* are deeper portions of the stream where water flows more slowly over a bed of fine sediments. Biological communities in lotic ecosystems are associated with different physical locations within the stream and their related environments (**Figure 3.14**). Organisms that live in the flowing water of the main channel are generally

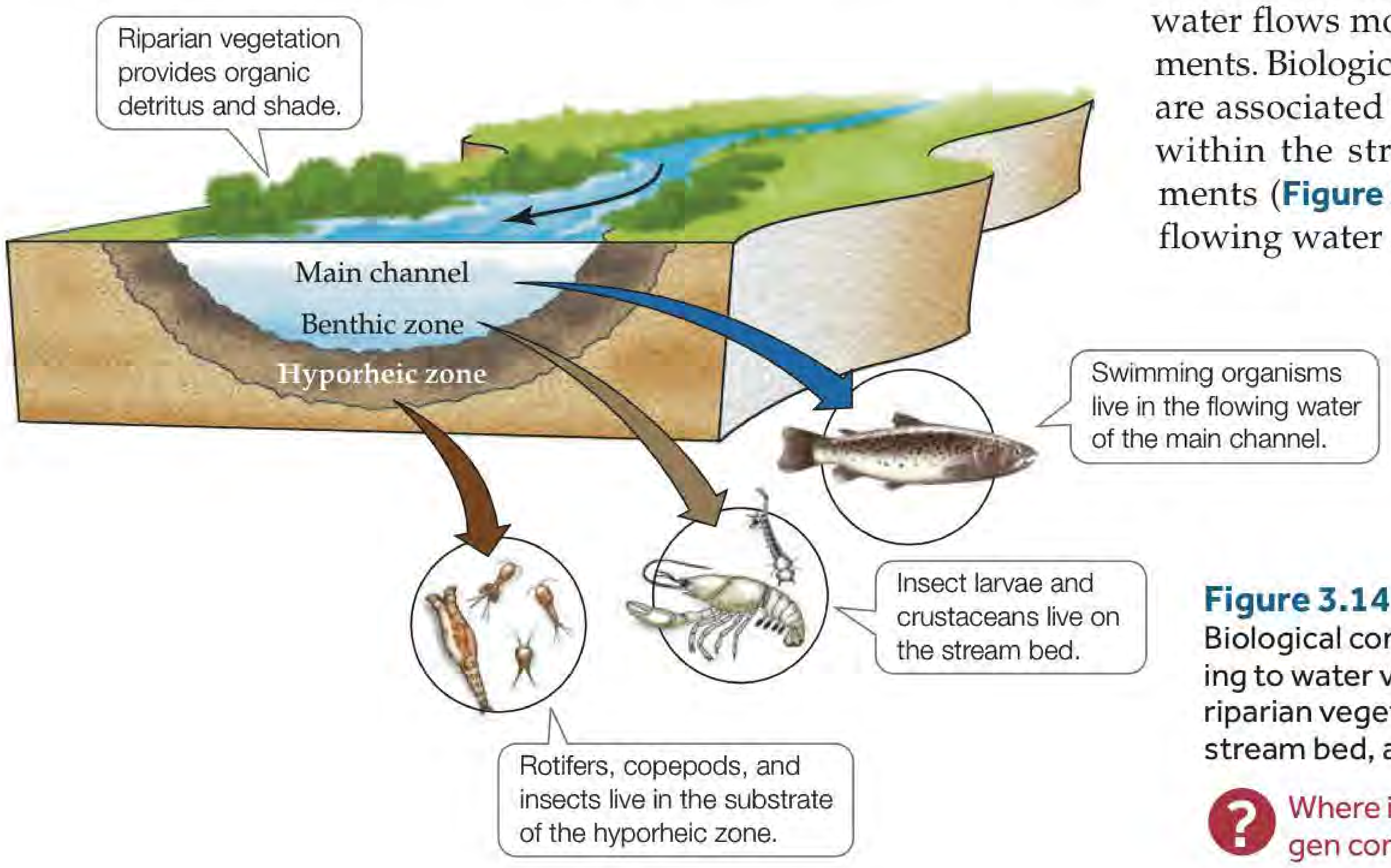


Figure 3.14 Spatial Zonation of a Stream Biological communities in a stream vary according to water velocity, inputs of plant material from riparian vegetation, the size of particles on the stream bed, and the depth of the stream.

? Where in this stream would you expect oxygen concentrations to be highest and lowest?

swimmers, such as fish. The bottom of the stream, called the **benthic zone**, is home to invertebrates; some of these, such as some mayfly and fly (dipteran) larvae, consume **detritus** (dead organic matter), and some, such as some caddisflies and crustaceans, hunt other organisms. Some organisms, such as rotifers, copepods, and insects, are found in the substrate below and adjacent to the stream, where water, either from the stream or from groundwater moving into the stream, still flows. This area is known as the **hyporheic zone**.

The composition of biological communities in streams and rivers changes with stream order (see Figure 3.13) and channel size. The *river continuum concept* was developed to describe these changes in both the physical and biological characteristics of a stream (Vannote et al. 1980). This conceptual model holds that as a stream flows downslope and increases in size, the input of detritus from the vegetation adjacent to the stream (known as *riparian vegetation*) decreases relative to the volume of water, and the particle size in the stream bed decreases, from boulders and coarse rock in the higher portions to fine sand at the lower end, facilitating greater establishment of aquatic plants in the downstream direction. As a result, the importance of terrestrial vegetation as a food source for stream organisms decreases in the downstream direction. Coarse terrestrial detritus is most important near the stream source, while the importance of fine organic matter, algae, and rooted and floating aquatic vascular plants (known as **macrophytes**, from *macro*, "large"; *phyte*, "plant") increases downstream. The general feeding styles of organisms change accordingly as the river flows downstream. *Shredders*, organisms able to tear up and chew leaves (e.g., some species of caddisfly larvae), are most abundant in the higher parts of the stream, while *collectors*, organisms that collect fine particles from the water (e.g., some dipteran larvae), are most abundant in the lower parts of the stream. The river continuum concept applies best to temperate river systems, but not as well in boreal, Arctic, or tropical rivers or in rivers with high concentrations of dissolved organic substances (including tannic and humic acids) derived from wetlands. Nonetheless, the model provides a basis for studying biological organization in stream and river systems.

Human effects on lotic ecosystems have been extensive. Most fourth- and higher-order rivers have been altered by human activities, including pollution, increases in inputs of sediments, and introductions of non-native species. Streams and rivers have been used as conduits for the disposal of sewage and industrial wastes in most parts of the world inhabited by humans. These pollutants often reach levels that are toxic to many aquatic organisms. Excessive application of fertilizers to croplands results in runoff into rivers as well as leaching of nutrients into groundwater that eventually reaches rivers. Inputs of nitrogen and phosphorus from fertilizers alter the composition of aquatic communities. Deforestation increases inputs of stream sediment, which can reduce water clarity, alter benthic habitat, and inhibit gill function in many aquatic organisms. Introductions of non-native species, such as sport fishes (e.g., bass and trout), have lowered the diversity of native species in both stream and lake ecosystems. The construction of dams on streams and rivers tremendously alters their physical and biological properties, converting them into still waters—the topic of the next section.

Biological communities in lakes vary with depth and light penetration

Lakes and other still waters, called **lentic** ecosystems, occur where natural depressions have filled with water or where humans have dammed rivers to form reservoirs. Lakes and ponds may be formed when glaciers gouge out depressions and leave behind natural dams of rock debris (moraines), or when large chunks of glacial ice break off, become surrounded by glacial debris, and then melt. Most temperate and polar lakes are formed by glacial processes. Lakes may also form when meandering rivers cease to flow through a former channel, leaving a section stranded, called an *oxbow lake*. Geologic phenomena, such as extinct volcanic calderas and sinkholes, form natural depressions that may fill with water. Lakes and ponds of biological origin, in addition to reservoirs, include beaver dams and animal wallows.

Lakes vary tremendously in size, from small, ephemeral ponds to the massive Lake Baikal in Siberia, which is 1,600 m (5,200 feet) deep and covers 31,000 km^2 (12,000 square miles). The size of a lake has important consequences for its nutrient and energy status and therefore for the composition of its biological communities. Deep lakes with little surface area tend to be nutrient-poor compared with shallow lakes with much surface area (see Concept 22.4).

Lake biotic assemblages are associated with depth and degree of light penetration. The open water, or **pelagic zone**, is inhabited by **plankton**: small, often microscopic organisms that are suspended in the water (**Figure 3.15**). Photosynthetic plankton (called **phytoplankton**) are limited to the surface layer of water where there is enough light for photosynthesis, called the **photic zone. Zooplankton**—tiny animals and nonphotosynthetic protists—occur throughout the pelagic zone, as do other consumers such as bacteria and fungi, feeding on detritus as it falls through the water. Fish patrol the pelagic zone, scouting for food and predators that might eat them.

The nearshore zone where the photic zone reaches to the lake bottom is called the **littoral zone**. Here, macrophytes join with floating and benthic phytoplankton to produce energy by photosynthesis. Fish and zooplankton also occur in the littoral zone.

In the benthic zone, detritus derived from the littoral and pelagic zones serves as an energy source for animals,

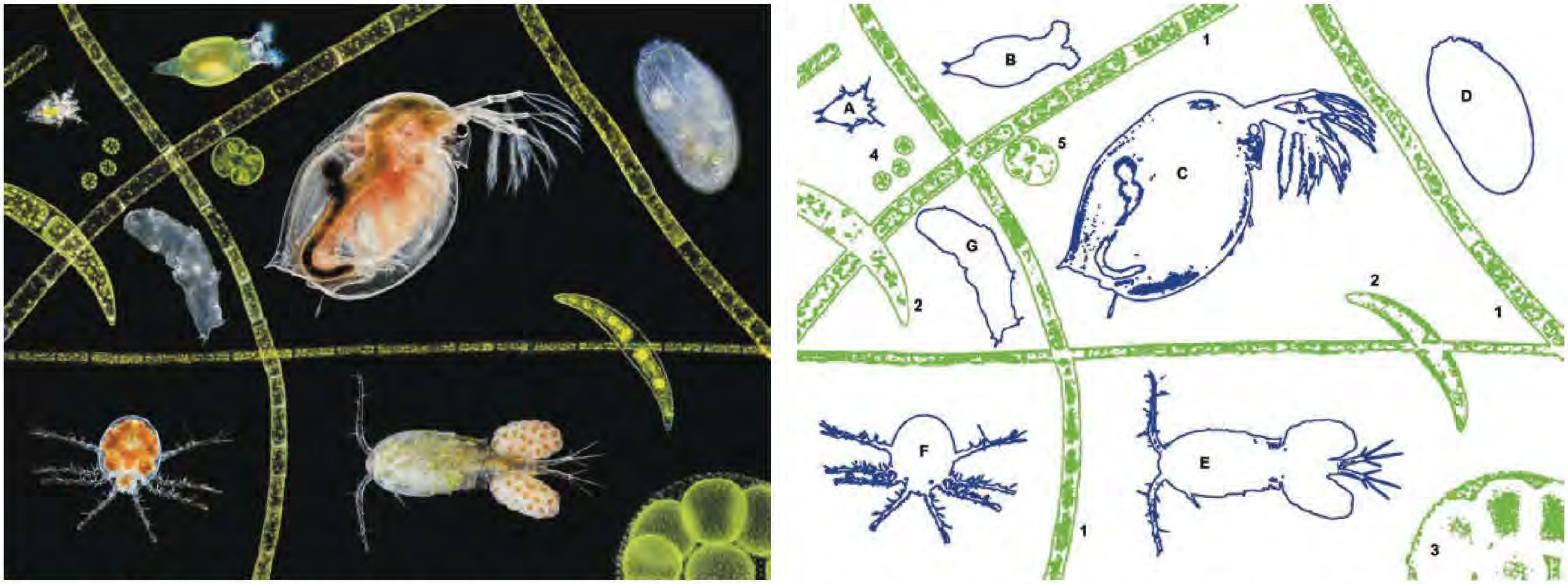


Figure 3.15 Examples of Lake Plankton In this composite image of plankton from a pond, phytoplankton (green in the key) include filamentous algae (1), *Closterium* sp. (2), *Volvox* sp. (3), and other green algae (4, 5). Zooplankton (blue in the key) include a larval copepod (A), rotifer (B), water flea (*Daphnia* sp., C), ciliated protist (D), adult copepod (*Cyclops* sp.) with egg sacs (E), mite (F), and tardigrade (G).

fungi, and bacteria. The benthic zone is usually the coldest part of the lake, and its oxygen concentrations are often low.

Let's move from fresh waters to the biological zones of the oceans. You will see that some of those zones have names and characteristics similar to those in freshwater lakes but have much greater spatial cover. As in freshwater communities, physical characteristics are used to differentiate marine biological zones.

CONCEPT 3.3
Marine biological zones are determined by ocean depth, light availability, and the stability of the bottom substrate.

Marine Biological Zones

Oceans cover 71% of Earth's surface and contain a rich diversity of life. The vast area and volume of the oceans and their environmental uniformity make them considerably different from terrestrial ecosystems in terms of biological organization. Marine organisms are more widely dispersed, and marine communities are not as easily organized into broad biological units as terrestrial biomes are. Instead, marine biological zones are coarsely categorized by their physical locations relative to shorelines and the ocean bottom (**Figure 3.16**). The distributions of the organisms that inhabit these zones reflect differences in temperature, as we saw for terrestrial biomes, as well as other important factors, including light availability, water depth, stability of the bottom substrate, and interactions with other organisms.

In this section, we will take a tour of the biological zones of the oceans, from the margins of the land to the deep, dark, cold ocean bottom. We will examine the physical and biological factors that characterize the different zones and the major organisms found in them.

Nearshore zones reflect the influence of tides and substrate stability

Marine biological zones adjacent to the continents are influenced by local climate, by the rise and fall of ocean

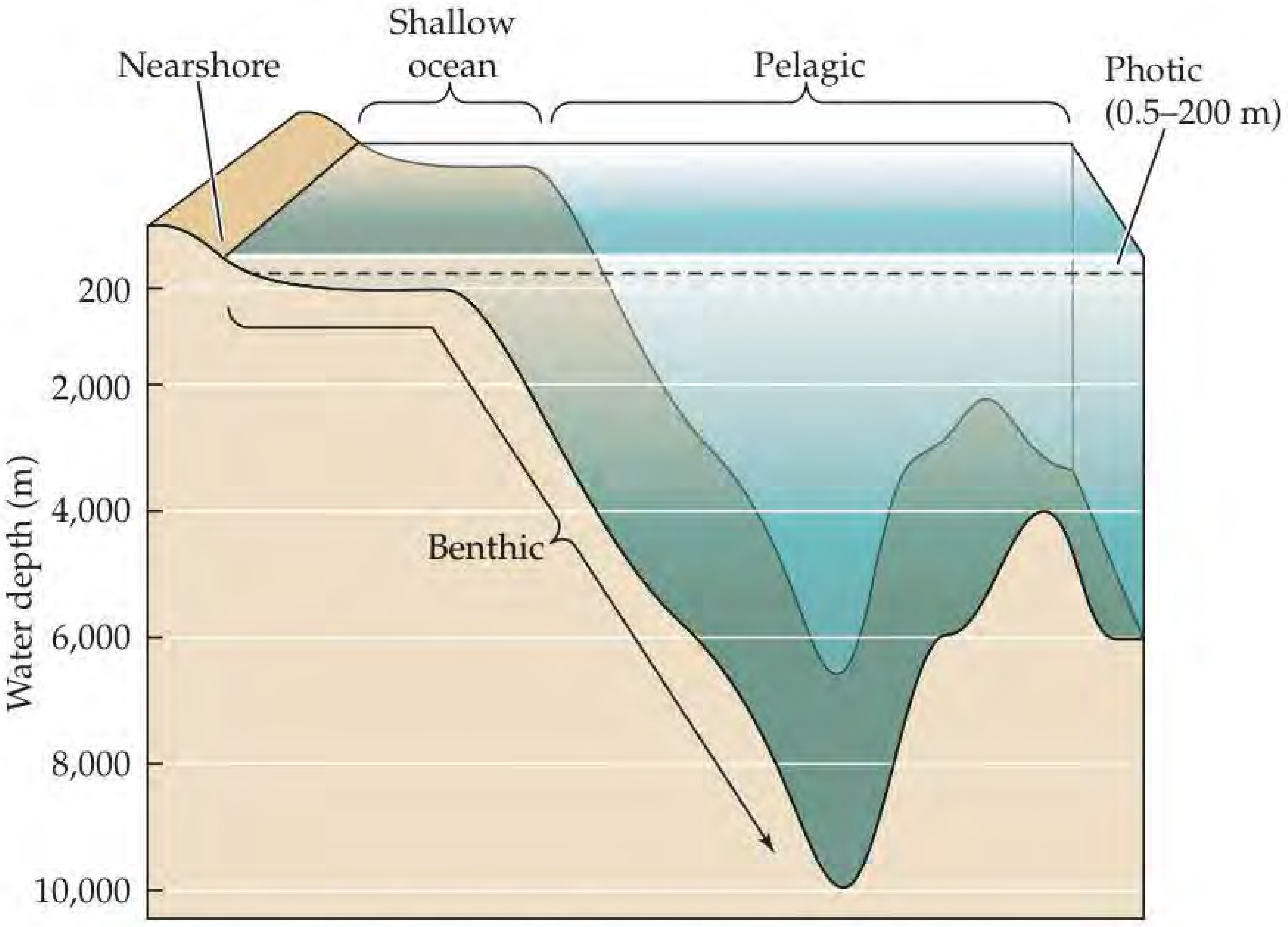


Figure 3.16 Marine Biological Zones Biological zones in the ocean are categorized by water depth and by their physical locations relative to shorelines and the ocean bottom.

waters associated with tides, and by wave action and the influx of fresh water and terrestrial sediments from rivers. **Tides** are generated by the gravitational attraction between Earth and the moon and sun. Ocean water rises and falls in most nearshore zones twice daily. The magnitude of the tidal range varies greatly among different locations because it is related to shoreline morphology and ocean bottom structure. Tides produce unique transition zones between terrestrial and marine environments and influence salinity and nutrient availability in these nearshore habitats.

ESTUARIES The junction of a river with the ocean is called an *estuary* (**Figure 3.17**). Estuaries are characterized by variations in salinity associated with the flow of fresh river water into the ocean and the influx of salt water flowing inland from the ocean as tides rise. Rivers bring terrestrial sediments containing nutrients and organic matter to the ocean, and the interaction of tidal and river flows acts to trap these sediments in estuaries, enhancing their productivity. The varying salinity of estuaries is an important determinant of the organisms that occur there. Many commercially valuable fish species spend their juvenile stages in estuaries, away from fish predators that are not as tolerant of the changes in salinity. Other inhabitants of estuaries include shellfish (e.g., clams and oysters), crabs, marine worms, and seagrasses. Estuaries are increasingly threatened by water pollution carried by rivers. Nutrients from upstream agricultural sources can cause local dead zones (see Concept 25.3) and losses of biological diversity.

Figure 3.17 Estuaries Are Junctions between Rivers and Oceans The mixing of fresh and salt water gives estuaries a unique environment with varying salinity. Rivers bring in energy and nutrients from terrestrial ecosystems.

Figure 3.18 Salt Marshes Are Characterized by Salt-Tolerant Vascular Plants Emergent vascular plants form salt marshes in shallow nearshore zones.

SALT MARSHES Terrestrial sediments carried to shorelines by rivers form shallow marsh zones (**Figure 3.18**) that are dominated by vascular plants that rise out of the water, including grasses, rushes, and broad-leaved herbs. In these salt marshes, as in the estuaries that they often border, the input of nutrients from rivers enhances productivity. Periodic flooding of the marsh at high tide results in a gradient of salinity: the highest portions of the marsh can be the most saline because infrequent flooding and evaporation of water from the soil lead to a progressive buildup of salts. Salt marsh plants grow in distinct zones that reflect this salinity gradient, with the most salt-tolerant species in the highest portions of the marsh. Salt marshes provide food and protection from predators for a wide variety of animals, including fish, crabs, birds, and mammals. Organic matter trapped in salt marsh sediments may serve as a nutrient and energy source for nearby marine ecosystems.

MANGROVE FORESTS Shallow coastal estuaries and nearby mudflats in tropical and subtropical regions are inhabited by salt-tolerant evergreen trees and shrubs (**Figure 3.19**). These woody plants are collectively referred to as mangroves, but "mangroves" include species from 16 different plant families, not a single taxonomic group. Mangrove roots trap mud and sediments carried by the water, which build up and modify the shoreline. Like salt marshes, mangrove forests provide nutrients to other marine ecosystems and habitat for numerous animals, both marine and terrestrial. Among the unique animals associated with mangroves are manatees, crab-eating monkeys, fishing cats, and monitor lizards. Mangrove

Figure 3.19 **Salt-Tolerant Evergreen Trees and Shrubs Form Estaurine Mangrove Forests** The mangrove roots trap mud and sediments and provide habitat for other marine organisms.

forests are threatened by human development of coastal areas—particularly the development of shrimp farms—as well as by water pollution, diversion of inland freshwater sources, and cutting of the forests for wood.

ROCKY INTERTIDAL ZONES Rocky shorelines provide a stable substrate to which a diverse collection of algae and animals can anchor themselves to keep from being washed away by the pounding waves (**Figure 3.20**). The physical environment of the **intertidal** zone—the part of the shoreline affected by the rise and fall of the tides—alternates between marine and terrestrial. Between the high- and low-tide marks, a host of organisms are arranged in zones associated with their tolerance for temperature changes, salinity, *desiccation* (drying out), wave action, and interactions with other organisms. *Sessile* (attached) organisms such as barnacles, mussels, and seaweeds must cope with these stresses in order to survive. Mobile organisms, such as sea stars and sea urchins, may move to tide pools in order to minimize exposure to these stresses.

SANDY SHORES Except for a few scurrying crabs and shorebirds and the occasional bit of seaweed washed ashore, sandy beaches appear devoid of life. Unlike the rocky shore, the sandy substrate provides no stable anchoring surface, and the lack of attached seaweeds limits the supply of potential food for herbivorous animals. Tidal fluctuations and wave action further limit the potential for the development of biological communities. Beneath the sand, however, invertebrates such as clams, sea worms, and mole crabs find suitable habitat (**Figure 3.21**). Smaller organisms, such as polychaete worms, hydroids (small animals related to jellyfishes), and copepods (tiny crustaceans), live on or among the grains of sand. These organisms are protected from temperature changes and desiccation at low tide and from the turbulent water at high tide. When the sand is immersed in seawater, some of these organisms emerge to feed on detritus or other organisms, while others remain buried and filter detritus and plankton from the water.

Shallow ocean zones are diverse and productive

Near the coastline, enough light may reach the ocean bottom to permit the establishment of sessile photosynthetic organisms. Like terrestrial plants, these photosynthetic organisms provide energy that supports communities of animals and microorganisms, as well as a physical structure that creates habitat for those organisms, including surfaces to which they can anchor and places where they can find refuge from predators. The diversity and complexity of the habitats provided by the photosynthesizers support

Figure 3.20 **The Rocky Intertidal Zone: Stable Substrate, Changing Conditions** Rocky shorelines provide a stable substrate to which organisms can anchor themselves, but those organisms must cope with the shift from terrestrial to marine conditions that occurs with each tide, as well as wave action. Sessile organisms must be resistant to temperature changes and desiccation. Mobile organisms often take refuge in tide pools to avoid exposure to the terrestrial environment.

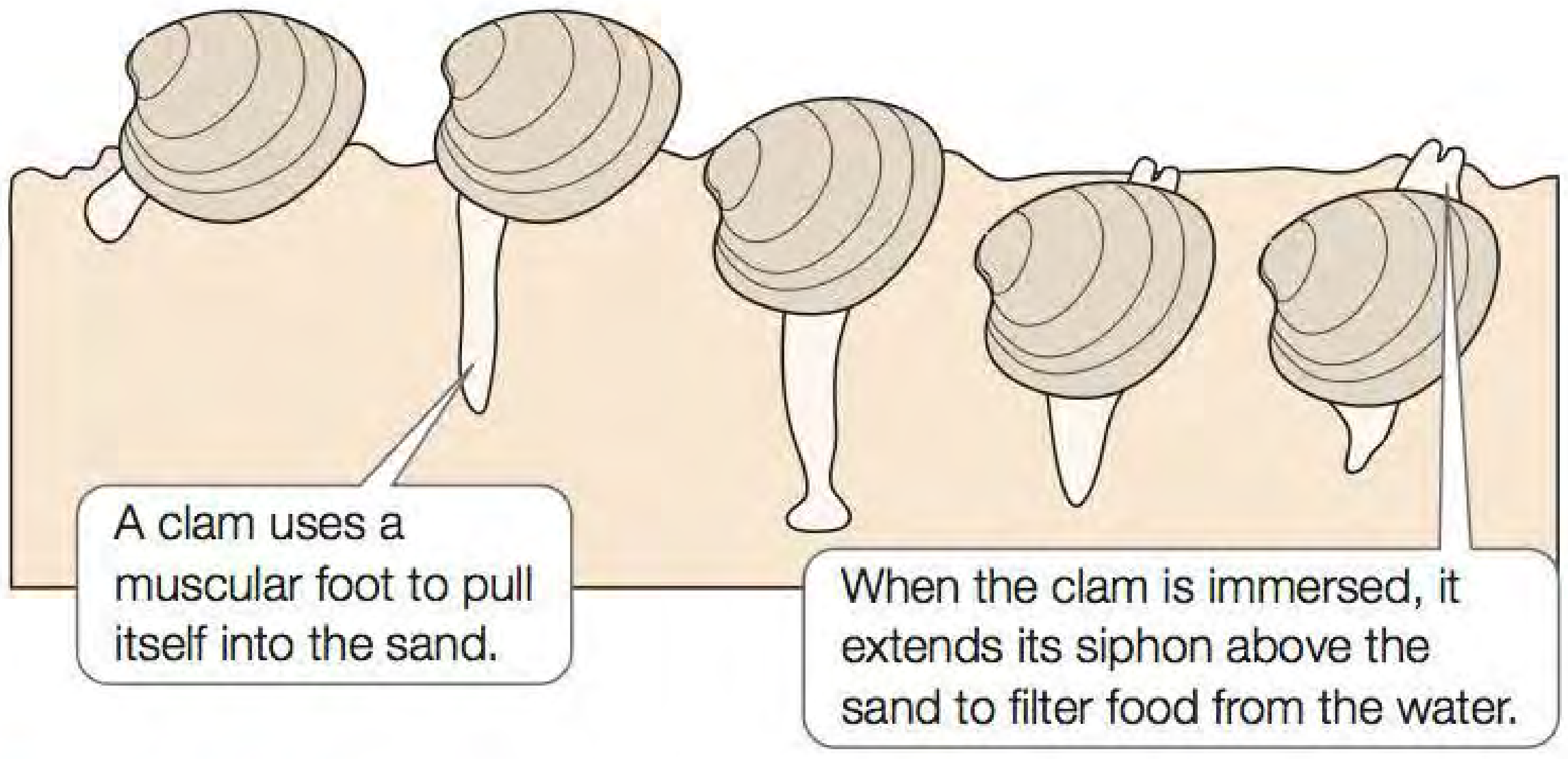


Figure 3.21 Burrowing Clams Clams, like most animals of sandy shorelines, live in the sandy substrate.

considerable biological diversity in these shallow ocean environments.

CORAL REEFS In warm, shallow ocean waters, corals (animals related to jellyfishes), living in a close association with algal partners (a symbiotic mutualism; see Concept 15.1), form large colonies. The corals obtain most of their energy from algae that live within their bodies, while the algae receive protection from grazers and some nutrients from the corals. Many corals build a skeleton-like structure by extracting calcium carbonate from seawater. Over time, these coral skeletons pile up into massive formations called *reefs* (**Figure 3.22**). The formation of reefs is aided by other organisms that extract other minerals from seawater, such as sponges that precipitate silica. The unique association of these reef-building organisms gives rise to a structurally complex habitat that supports a rich marine community.

Figure 3.22 A Coral Reef Corals create habitat for a diverse assemblage of marine organisms.

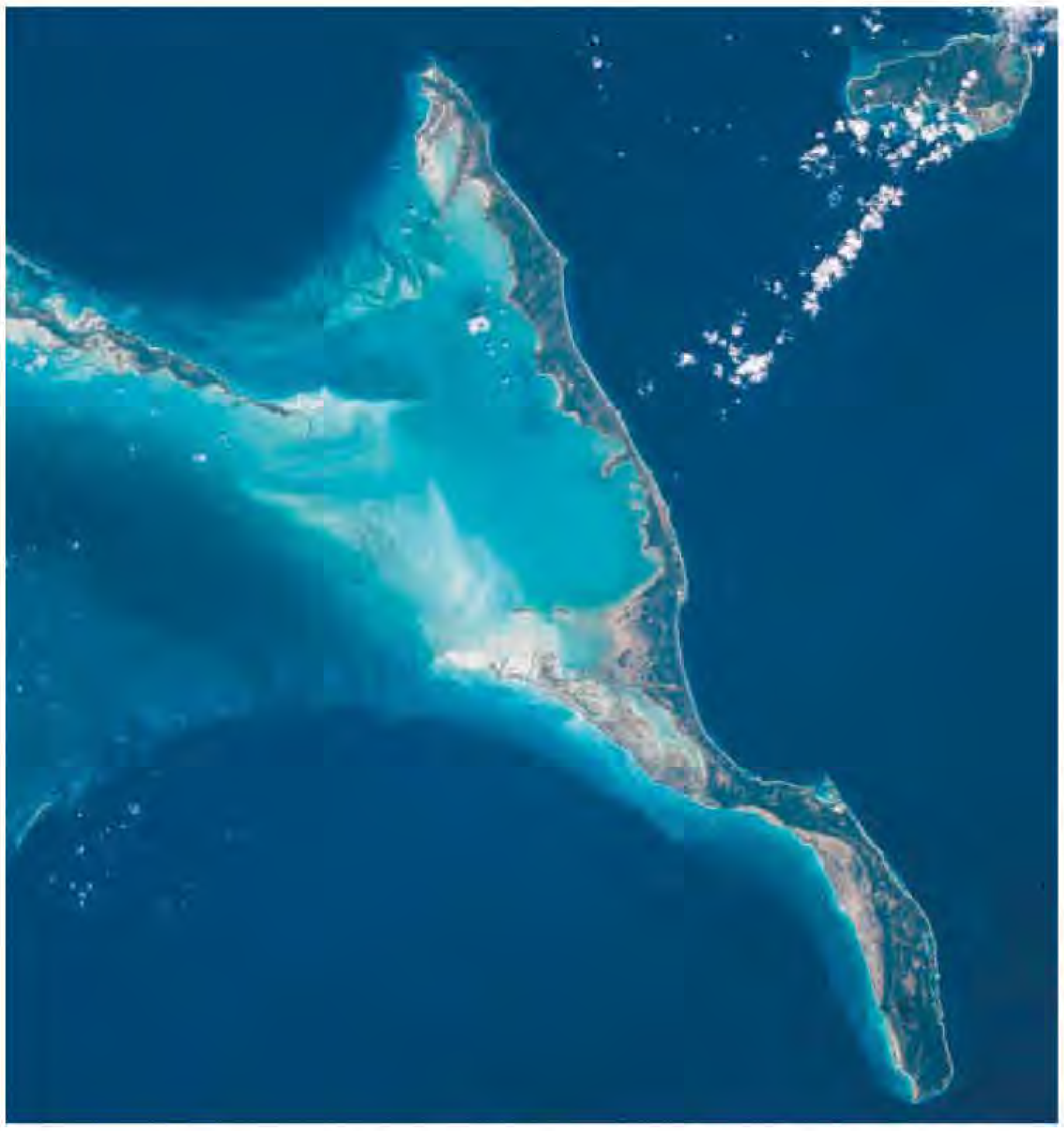


Figure 3.23 Coral Reefs Can Be Seen from Outer Space Long Island, in the Bahamas, was formed by coral reefs, which can be seen on the fringes of the island in this satellite photograph.

Coral reefs grow at rates of only a few millimeters per year, but they have shaped the face of Earth (Birkeland 1997). Over millions of years, corals have constructed thousands of kilometers of coastline and numerous islands (**Figure 3.23**). The rate of production of living biomass in coral reefs is among the highest on Earth. The accretions of coral skeletons are as much as 1,300 m (4,300 feet) thick in some places, and they currently cover a surface area of 600,000 km^2 (23,000 square miles), approximately 0.2% of the ocean surface.

As many as a million species are found in coral reefs worldwide, including more than 4,000 fishes. Many economically important fish species rely on coral reefs for habitat, and reef fishes provide a source of food for fishes of the open ocean, such as jacks and tuna. The taxonomic and morphological diversity of animals in coral reefs is greater than in any other ecosystem on Earth (Paulay 1997). The full diversity of coral reefs has yet to be explored and described, however. The potential for development of medicines from coral reef organisms is great enough that the U.S. National Institutes of Health established a laboratory in Micronesia to explore it.

Human activities threaten the health of coral reefs in a number of ways. Sediments carried by rivers can cover and kill the corals, and excess nutrients increase the growth of algae on the surfaces of the corals, increasing coral mortality. Changes in ocean temperatures associated with climate change can result in the loss of the corals' algal partners, a condition called *bleaching*. Increased atmospheric CO_2 has increased ocean acidification (discussed in more detail in Concept 25.1), which inhibits the ability of corals to form skeletons (Orr et al. 2005). Another threat is an increased incidence of fungal infections, possibly related to increased environmental stress.

SEAGRASS BEDS Although we typically associate flowering plants with terrestrial environments, some flowering plants are important components of shallow (<5 m) subtidal communities. These submerged flowering plants are called seagrasses, although they are not closely related to plants in the grass family. Morphologically, they are similar to their relatives on land, with roots, stems, and leaves as well as flowers, which are pollinated under water. Seagrass beds are found on subtidal marine sediments composed of mud or fine sand. The plants reproduce primarily by vegetative growth, although they produce seeds as well. Marine algae and animals grow on the surfaces of the plants, and the larval stages of some organisms, such as mussels, are dependent on them for habitat. Inputs of nutrients from upstream agricultural activities can harm seagrass beds by increasing the density of algae in the water and on the surfaces of the seagrasses. Seagrasses are also susceptible to periodic outbreaks of fungal diseases.

Figure 3.24 A Kelp Bed Giant kelp are brown algae (order Laminariales) that attach themselves to the solid bottom in shallow ocean waters, providing food and habitat for many other marine organisms.

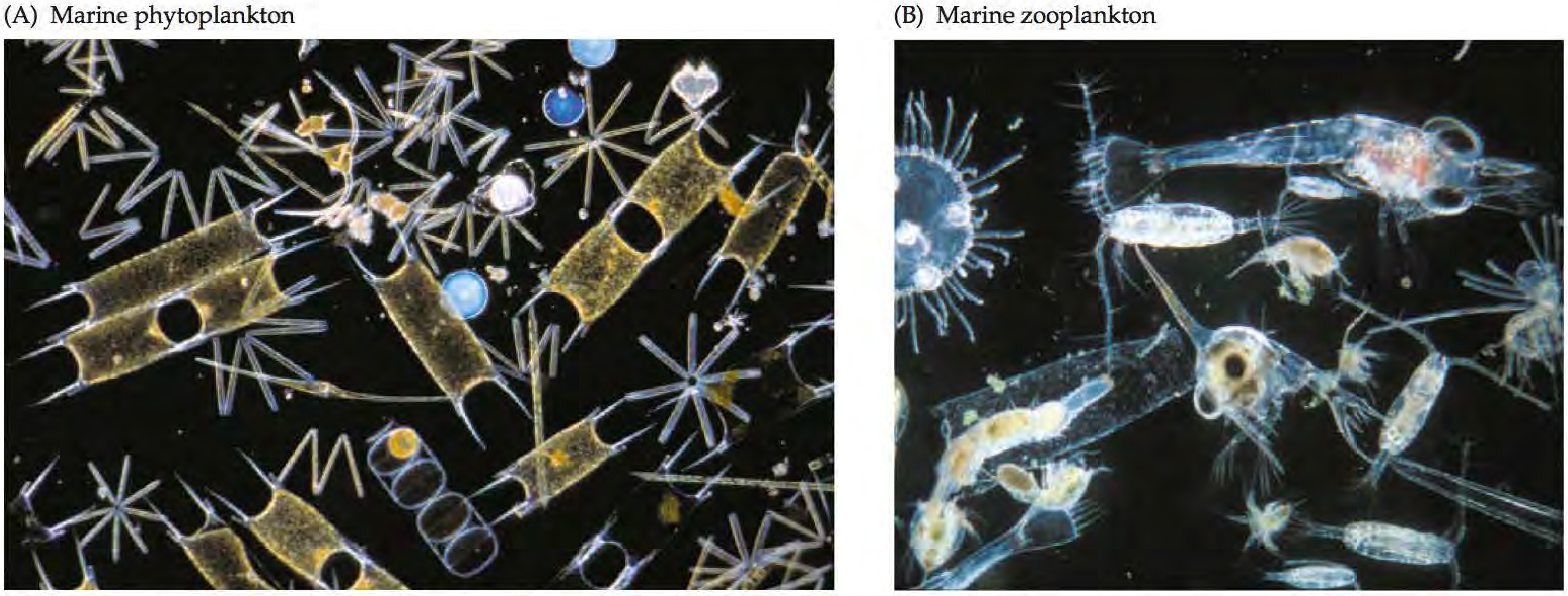
KELP BEDS In clear, shallow (<15 m) temperate ocean waters, large stands of seaweed, known as kelp beds or kelp forests (**Figure 3.24**), support a rich and dynamic community of marine life. Kelp are large brown algae of several different genera. They have specialized tissues resembling leaves (fronds), stems (stipes), and roots (holdfasts). Kelp are found where a solid substrate is available for anchoring. Residents of kelp beds include sea urchins, lobsters, mussels, abalones, numerous other seaweeds, and sea otters. Interactions among these organisms, both direct and indirect, influence the abundance of the kelp (see the Case Study in Chapter 9). In the absence of grazing, kelp beds can become so dense that light reaching the bottom of the canopy is not sufficient to support photosynthesis.

Open ocean and deep benthic zones are determined by light availability and proximity to the bottom

Beyond the continental shelves, the vastness and depth of the open ocean, known as the pelagic zone, make it difficult to differentiate distinct biological communities there. Light availability determines where photosynthetic organisms can occur, which in turn determines the availability of food for animals and microorganisms. Thus, the surface waters with enough light to support photosynthesis (the photic zone) contain the highest densities of organisms (see Figure 3.16). The photic zone extends about 200 m downward from the ocean surface, depending on water clarity. Below the photic zone, the supply of energy, mainly in the form of detritus falling from the photic zone, is much lower, and life is far less abundant.

The diversity of life in the pelagic zone varies considerably. Its **nekton** (swimming organisms capable of overcoming ocean currents) include cephalopods such as squids and octopuses, fishes, sea turtles, and mammals such as whales and porpoises. Most of the photosynthesis in the pelagic zone is carried out by phytoplankton, which include green algae, diatoms, dinoflagellates, and cyanobacteria (**Figure 3.25A**). Zooplankton include protists such as ciliates, crustaceans such as copepods and krill, and jellyfishes (**Figure 3.25B**). Many species of pelagic seabirds, including albatrosses, petrels, fulmars, and boobies, spend the majority of their lives flying over open ocean waters, feeding on marine prey (fish and zooplankton) and detritus found on the ocean surface.

Organisms that live in the pelagic zone must overcome the effects of gravity and water currents that could force them to progressively greater depths. Photosynthetic organisms, and those directly dependent on them as a food source, must stay in the photic zone where sunlight is sufficient to maintain photosynthesis, growth, and reproduction. Swimming is an obvious solution to this problem, used by organisms such as fishes and squids.


(A) Marine phytoplankton

(B) Marine zooplankton

Figure 3.25 Plankton of the Pelagic Zone (A) This sample of marine phytoplankton includes several species of diatoms, including *Biddulphia sinensis* (the rectangular cells with the concave ends) and *Thalassiothrix*. (B) These marine zooplankton include adult copepods and the larval stages of various organisms, including the zoea (spherical) larva of a crab.

Seaweeds such as *Sargassum* and some fish species have gas-filled bladders that keep them buoyant. Large mats of *Sargassum* sometimes form "floating islands" that host rich and diverse biological communities. Some plankton retard their sinking by decreasing their density relative to seawater (e.g., through alteration of their chemical composition) or through shapes that lower their downward velocity (e.g., having a cell wall with projections).

Beneath the photic zone, the availability of energy decreases, and the physical environment becomes more demanding as temperatures drop and water pressure rises. As a result, organisms are few and far between. Crustaceans such as copepods graze on the rain of falling detritus from the photic zone. Crustaceans, cephalopods, and fishes are the predators of the deep sea. Some fishes take on frightening forms, appearing to be mostly mouth (**Figure 3.26**). The meanings of the scientific names given to some of the sea creatures at this depth, such as "vampire squid from hell" (*Vampyroteuthis infernalis*), "stalked toad with many filaments" (*Caulophryne polynema*), and "Prince Axel's wonder fish" (*Thaumatichthys axeli*), testify to the unusual forms found there. Most deep-sea fishes have weak bone structure to reduce their weight and lack the gas bladder found in most fishes, since the high pressures would collapse it.

The ocean bottom (the benthic zone) is also very sparsely populated. Temperatures are near freezing, and pressures are great enough to crush any terrestrial organism. Conversely, if deep-sea creatures adapted to these high pressures are brought to the surface, their bodies may expand and burst. The sediments of the benthic zone, which are rich in organic matter, are inhabited by bacteria and protists as well as sea worms. Sea stars and sea cucumbers graze the ocean floor, consuming organic matter or organisms in the sediments or filtering food from the water. Benthic predators, like those of the deep pelagic zone, use bioluminescence to lure prey. Because of the logistic difficulties involved, the deep-sea benthic zone is one of the least explored and poorly understood marine biological zones.

Figure 3.26 A Denizen of the Deep Pelagic Zone Anglerfish (*Melanocetus* spp.) are named for their unique strategy for capturing prey. In the lightless depths, the bioluminescent organ on the fish's forehead attracts prey to a position where they are easily engulfed by the huge, tooth-filled mouth.

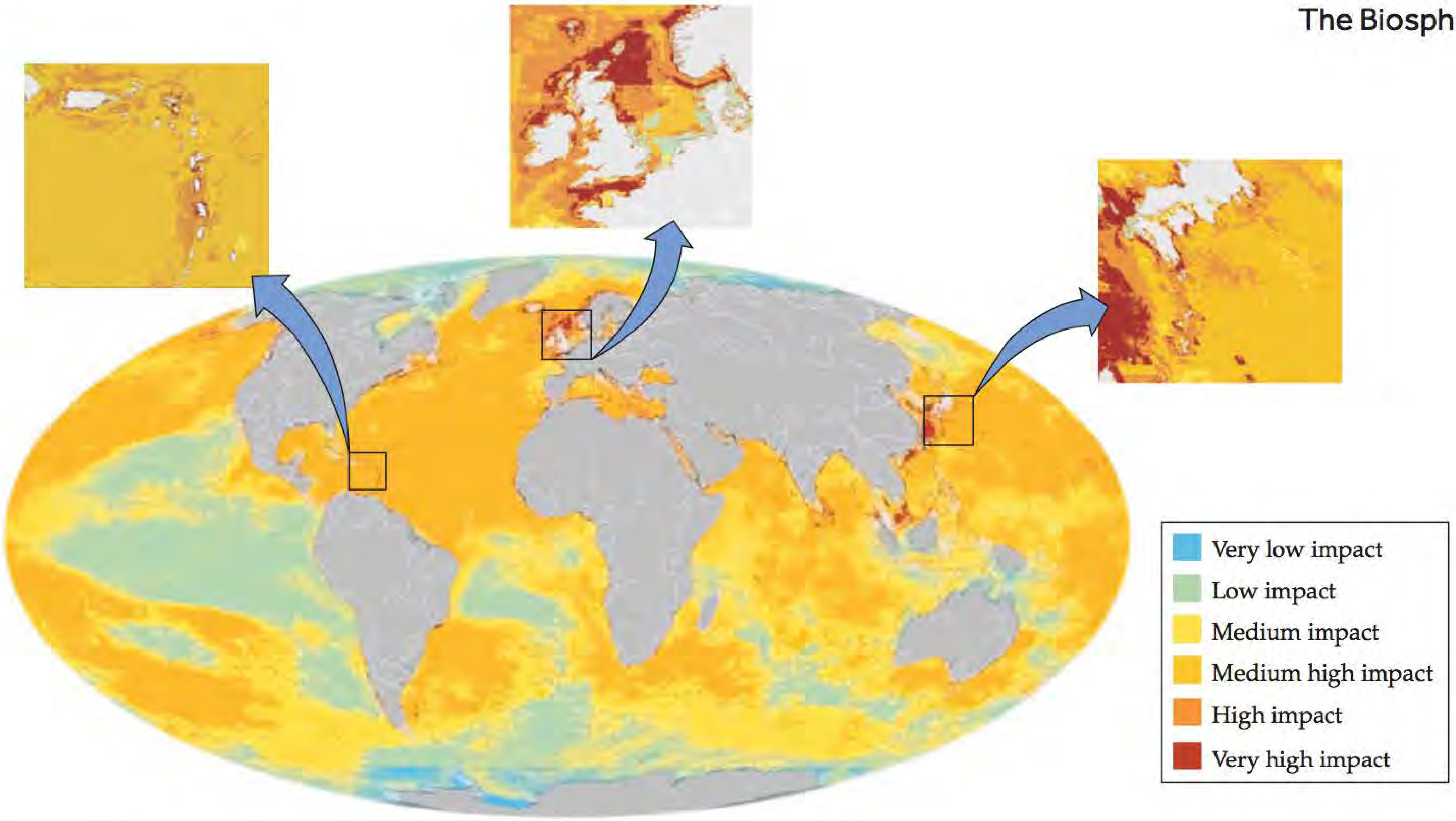


Figure 3.27 **Human Impacts on the Oceans** The impacts of greenhouse gas emissions, pollutant inputs, and overfishing have varied in different regions of the oceans. The colors represent the degree of impact, which was quantified using expert judgments of 17 different environmental impact factors. The enlarged areas from the Caribbean Sea (left), North Atlantic Ocean (center), and western Pacific Ocean (right) show greater detail of more heavily impacted areas. Note the correspondence between the areas of high and very high impact with areas of significant human impact in the adjacent terrestrial regions in Figure 3.5. (From Halpern et al. 2008.)

Marine biological zones have been impacted by human activities

Our discussion of marine biological zones has alluded to several services they provide to humans, including food production (e.g., fisheries in the nearshore and open ocean zones), protection of coastal areas from erosion (e.g., mangrove forests), uptake and stabilization of pollutants and nutrients (estuaries and marshes), and recreational benefits (Barbier et al. 2011). These services, along with ocean biodiversity, are increasingly threatened by human activities.

Despite the vastness of the ocean, human activities have affected it to varying degrees over the majority of its area (**Figure 3.27**). These include land-based activities that release nutrients and pollutants into rivers, ocean-based activities such as commercial fishing, and emissions of greenhouse gases. The effects of these activities include changes in water temperature and ocean acidification due to increases in greenhouse gases, increases in UV radiation due to the loss of protective stratospheric ozone, inputs of pollutants, and overharvesting of sea creatures, particularly fishes and whales (Halpern et al. 2008). (See Concepts 25.2 and 25.4 for more discussion of ozone loss and the greenhouse effect.) These impacts have the potential to influence the services on which humans depend, as well as the composition and abundance of the biota that inhabit different marine biological zones. The greatest estimated impacts are in nearshore marine ecosystems (estuaries, rocky intertidal zones, and sandy shores) near terrestrial regions that are sources of pollutants and nutrients, such as the regions adjacent to northern Europe and eastern Asia. Despite the widespread nature of human impacts, large areas of the ocean remain only moderately affected, and greater recognition of these impacts could lead to increased conservation and more sustainable use of ocean resources.

A CASE STUDY REVISITED

The American Serengeti—Twelve Centuries of Change in the Great Plains

Humans have been implicated in several major biological changes in the grasslands of the world. One of the earliest was the disappearance of large mammals from North America during the late Pleistocene. Paul Martin, an early proponent of this hypothesis, noted the strong correspondence between extinction events on several continents and the arrival of humans on those continents, principally Europe, North and South America, and Australia (Martin 1984, 2005). Martin suggested that the rapidity of the extinctions and the greater proportion of large animals that disappeared reflected the hunting efficiency of those early humans. Larger animals have lower reproductive rates than smaller animals, so they cannot recover from increases in predation as quickly. Martin's suggestion therefore took on the unfortunate label of "the overkill hypothesis."

Since it was first proposed, the overkill hypothesis has received increasing support. Archeological research has uncovered numerous butchering sites containing remains of extinct animals. Spearheads have been found among the bones, and some of the bones have scrape marks made by tools found at the sites. Other strong evidence indicates that human arrival on small, isolated oceanic islands led to large numbers of extinctions due to predation by humans and by other animals they introduced (e.g., rats and snakes). While most scientists now accept that hunting of megafauna by humans had a role in some of the continental extinctions in the late Pleistocene, other causes have been proposed as well. These causes include the spread of diseases carried by humans and possibly by the domesticated dogs that accompanied them (MacPhee and Marx 1997). Another hypothesis suggests that the loss of some animals on which other species depended, such as mastodons, led to more widespread extinctions (Owen-Smith 1987). No one hypothesis explains the extinctions of all the megafauna on all the continents, however. A combination of climate change and the arrival of humans probably contributed to their demise (Barnosky et al. 2004).

Although the diversity of large mammals on the Great Plains was greatly diminished following the Pleistocene, large mammals were still abundant. Bison may have numbered 30 million, and numerous elk (wapiti), pronghorn, and deer roamed the plains. These animals continued to be hunted by humans, who also began to use fire on the eastern edge of the Great Plains as a tool for managing the habitat of their prey, as well as for small-scale agriculture (Delcourt et al. 1998). The writings of travelers to the Great Plains in the early 1800s indicate that the western edge of the eastern deciduous forest was farther east than it is today, probably because of the influence of human-set fires.

Figure 3.28 Buffalo Hunting The arrival of large numbers of Euro-Americans in the Great Plains in the nineteenth century led to a mass slaughter of bison, facilitated by the construction of railroad lines and the use of high-powered rifles.

Between 1700 and 1900, ecological changes occurred in the Great Plains that profoundly transformed both the plants and the animals. The reintroduction of horses into North America by Spanish explorers facilitated the development of a Native American culture centered on the hunting of bison. The arrival of Euro-Americans, and their subsequent conflicts with Native Americans, led to the near extinction of bison and other large Plains animals by the late 1800s (**Figure 3.28**). With the arrival of cattle and mechanized agriculture after 1850, the Great Plains became a domesticated landscape. The moister eastern tallgrass prairie was converted into monocultures of corn, wheat, soybeans, and other crops; today, only 4% of that grassland remains. A larger proportion of the mixed-grass and short-grass prairies to the west remained intact, but overgrazing and unsustainable agricultural practices led to serious degradation of some of these areas during the Dust Bowl of the 1930s, when drought and massive windstorms resulted in substantial losses of fertile topsoil (see the Case Study in Chapter 25).

CONNECTIONS IN NATURE
Long-Term Ecological Research

Most terrestrial biomes and marine biological zones across the globe are experiencing changes due to human activities (see Figures 3.5 and 3.27 and **Online Climate Change Connection 3.1**). Even remote, seemingly pristine areas are subject to the effects of climate change and air pollution. Recognizing the effects of human activities on these systems, as well as our incomplete understanding of those effects, the U.S. National Science Foundation initiated the Long Term Ecological Research (LTER) Network of study sites in 1980. Initially consisting of 5 sites, the network has grown to 26 sites representing a diversity of terrestrial biomes, from tropical to polar, as well as marine biological zones, croplands, and urban centers (**Figure 3.29**). The formation of the U.S. LTER program has spurred the formation of an international network of LTER sites, facilitating international collaborative research to better understand Earth's ecological systems.

Long-term ecological research has advanced our understanding of ecological changes that occur at decadal and longer time scales. For example, research at LTER sites in the western United States has led to an understanding of the influence of the El Niño Southern Oscillation and the Pacific Decadal Oscillation (two climate cycles discussed in Concept 2.5) on the grassland biome. The legacy of climate change since the last glacial maximum, discussed in the Case Study at the opening of this chapter, is also better understood as a result of this research. Finally, research at LTER sites is providing a view of how environmental change, including climate change, may influence terrestrial biomes and marine biological zones in the future.

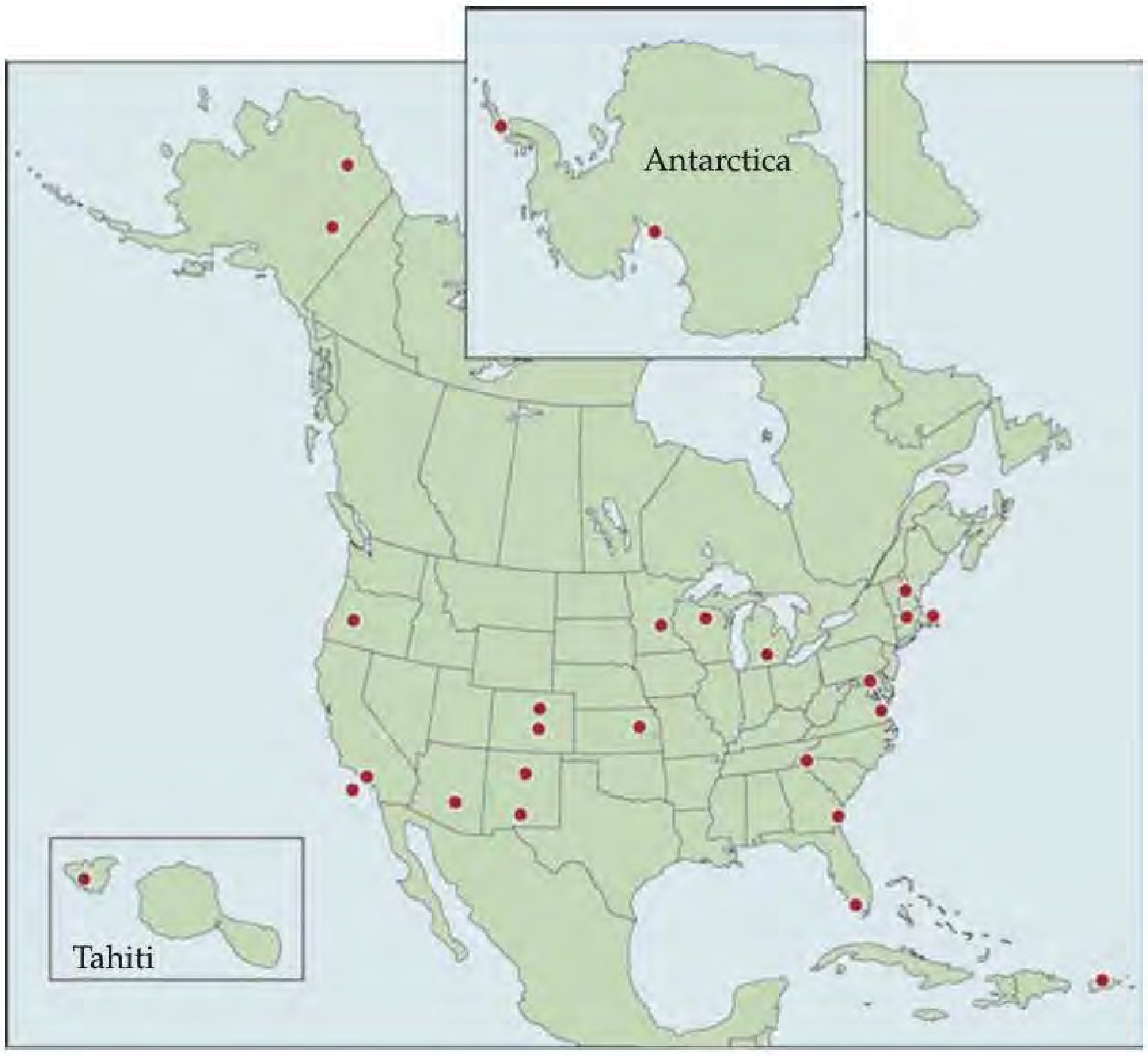


Figure 3.29 **Long-Term Ecological Research Sites** Twenty-six research sites constitute the U.S. Long Term Ecological Research (LTER) Network. These sites encompass deserts, grasslands, forests, mountains, lakes, estuaries, agricultural systems, and cities. Researchers measure long-term changes in ecosystems and perform experiments at these sites to better understand ecological dynamics over decades to centuries.

In this chapter, we've learned that grasslands are the biome most heavily impacted by human activities due to agricultural development. The Konza Prairie LTER site, located in the Flint Hills of northeastern Kansas, is a remnant tallgrass prairie—a very heavily impacted grassland type with very little of its original cover remaining. Research at the Konza Prairie site has focused on conserving this endangered biome in the face of rapid climate and land use change by examining the interactive roles of fire, grazing, and climate in the tallgrass prairie ecosystem. This research has included experiments varying the frequencies of fire and grazing in large landscape units to investigate their importance in maintaining the dominance of the grasses that characterize the grassland biome (**Figure 3.30**). Researchers have also examined the potential effects of changes in precipitation by varying the amount, intensity, and timing of watering. Results from this research have provided important insights into how climate change may affect the grassland biome, indicating that extremes in rainfall are important controls on its diversity and function (Knapp et al. 2002). Research at this and other LTER sites will enhance our ability to conserve native biodiversity in the face of accelerating environmental change.

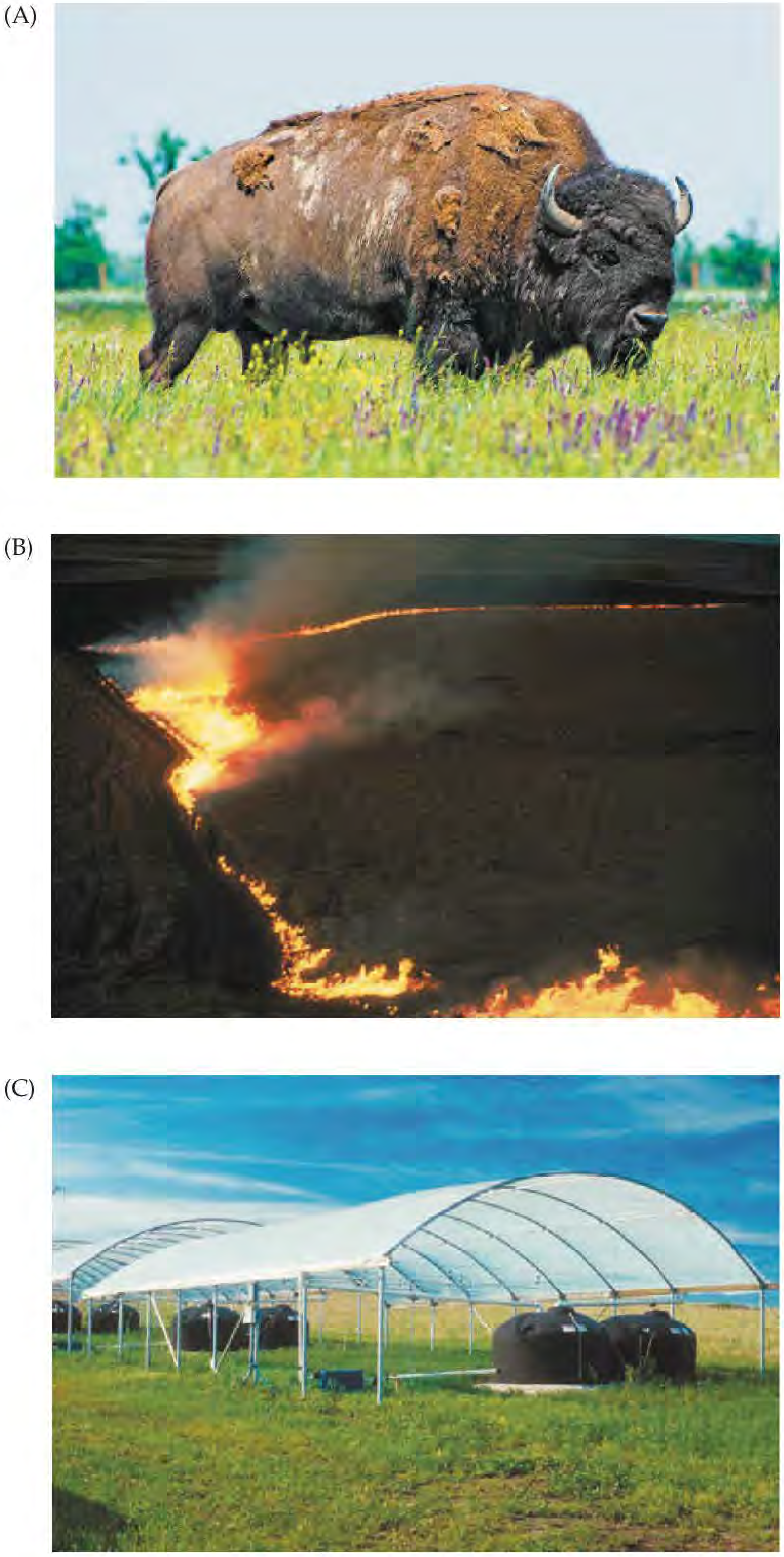


Figure 3.30 **Research at the Konza Prairie LTER Site** Long-term research and experiments are investigating the effects of the frequencies of (A) grazing, (B) fire, and (C) precipitation on the diversity and function of the tallgrass prairie ecosystem. (B,C courtesy of the Konza Prairie LTER.)

Summary

CONCEPT 3.1 Terrestrial biomes are characterized by the growth forms of the dominant vegetation.

- Terrestrial biomes are characterized by plant growth forms. These biomes reflect global patterns of precipitation and temperature.
- The potential and actual distributions of terrestrial biomes differ because of human activities, particularly conversion of land for agriculture, forestry, and grazing.
- There are nine major terrestrial biomes: tropical rainforests, tropical seasonal forests and savannas, and hot deserts in tropical and subtropical zones; grasslands, shrublands and woodlands, deciduous forests, and evergreen forests in the temperate zone; and boreal forests and tundra in polar regions.
- Biological communities in mountains occur in elevational bands associated with climate gradients.

CONCEPT 3.2 Biological zones in freshwater ecosystems are associated with the velocity, depth, temperature, clarity, and chemistry of the water.

- Biological communities in streams and rivers vary with stream order and location within the stream channel.
- Biological communities in lakes vary with depth and light penetration.

CONCEPT 3.3 Marine biological zones are determined by ocean depth, light availability, and the stability of the bottom substrate.

- Estuaries, salt marshes, and mangrove forests occur in shallow zones at the margins between terrestrial and marine ecosystems. They are influenced by inputs of fresh water and sediments from nearby rivers.
- Biological communities at the shoreline reflect the influence of tides and the stability of the substrate (sandy versus rocky).
- Coral reefs and kelp and seagrass beds are productive communities with high diversity associated with the habitat complexity provided by their photosynthesizers.
- Biological communities of the open ocean and deep benthic zones contain sparse populations of organisms, whose distributions are determined by light availability and proximity to the bottom.

Review Questions

1. Why are terrestrial biomes characterized using the growth forms of the dominant plants that occupy them?
2. Describe the close association between the distribution of biomes and the major climate zones described in Chapter 2. In particular, consider how seasonality of both temperature and precipitation influences biome distribution.
3. As streams flow from their source to the oceans, what physical changes occur that affect the distribution of their biological communities?
4. Why do ocean depth and the stability of the substrate play important roles in determining the composition of marine biological communities?

Hone Your Problem-Solving Skills

Chapter 2 introduced the concept of the rain-shadow effect on regional climates. Mountains intercepting air masses enhance precipitation on the windward slopes, with drier and warmer climates occurring on the leeward slopes. The change in temperature and precipitation with elevation therefore differs on west- versus east-facing slopes. The Cascade Range of the Pacific Northwest exemplifies this well. The windward west-facing slopes experience a temperature change with elevation (known as the environmental lapse rate) of 4.5°C per 1,000 m, while the leeward east-facing slopes have an environmental lapse rate of 6.5°C per 1,000 m.

1. Describe the vegetation types you would expect to encounter moving along a line from the base of the Cascade Range on the western side to the summit ridges at 3,000 m, and then descending to the bottom of the mountains on the eastern side. Use the information given in Figure 3.4 to determine the potential vegetation types. The annual average temperature for sites at the base of the west slopes (at sea level) is 12°C, and the average annual precipitation is 120 cm. Annual average precipitation on the summit ridges (3,000 m) increases to about 180 cm (assume the precipitation increase with elevation is linear). Annual average precipitation decreases to 50 cm at the base of the mountains on the leeward slope (elevation is 300 m).
2. Using the same approach you used in Question 1, describe the vegetation types you would expect to find along the same transect with the projected warming of 4°C and a 30% decrease in precipitation associated with climate change over the next 50 years.

ON THE COMPANION WEBSITE

ecology4e.sinauer.com

The website includes companions to all of the Analyzing Data exercises, Online Quizzes, Flashcards, Suggested Readings, and more. In addition, the following resources are available for this chapter:

Hands-On Problem Solving

3.1 Advance of the Tree Lines: Biome Boundaries and Climate Change

Online Climate Change Connection

3.1 Climate Change and the Development of Novel Biomes

4 Coping with Environmental Variation: Temperature and Water

KEY CONCEPTS

CONCEPT 4.1 Each species has a range of environmental tolerances that determines its potential geographic distribution.

CONCEPT 4.2 The temperature of an organism is determined by exchanges of energy with the external environment.

CONCEPT 4.3 The water balance of an organism is determined by exchanges of water and solutes with the external environment.

Frozen Frogs: A Case Study

In the movie *Austin Powers: International Man of Mystery*, a superspy of the 1960s voluntarily agrees to be cryonically frozen so that his talents can be tapped if Dr. Evil, his archnemesis who was frozen to avoid being caught by Austin, should reappear in the future. Indeed, 30 years later, both are unfrozen and continue their escapades of attempted and thwarted world domination.

The idea of suspended animation—life being put on hold temporarily—has captured the imagination and hopes of people waiting for medical science to develop ways to cure untreatable diseases or reverse the ravages of aging. *Cryonics* is the preservation of the bodies of deceased people at subfreezing temperatures with the goal of eventually bringing them back to life and restoring them to good health. Proponents of cryonics exist throughout the world, some more visible than others. In Nederland, Colorado, there is a yearly "Frozen Dead Guy Days" festival, considered to be the "Mardi Gras of cryonics." This festival commemorates the efforts of a former resident who had his grandfather frozen immediately after his death from heart failure, hoping that one day his grandfather could be brought back to life and given a heart transplant (as documented in the movie *Grandpa's Still in the Tuff Shed*).

To some, cryonics seems far-fetched, a thing of science fiction and comedy. Bringing life to a halt and then restarting it after a long period of quiescence doesn't seem plausible. Yet strange tales from nature provide examples of life apparently springing out of death. While seeking the existence of the Northwest Passage in the boreal and Arctic zones of Canada in 1769–1772, the English explorer Samuel Hearne found frogs under shallow layers of leaves and moss in winter "frozen as hard as ice, in which state the legs are as easily broken off as a pipe-stem" (Hearne 1911) (**Figure 4.1**). Hearne wrapped the frogs in animal skins and placed them next to his campfire. Within hours, the rock-hard amphibians came to life and began hopping around. The American naturalist John Burroughs found frozen frogs under a shallow cover of dead leaves in a New York forest in winter. Return visits to the same locations over a period of months indicated that the frogs hadn't moved, yet by spring they had disappeared. Could a complex organism like a frog, with a sophisticated circulatory and nervous system, have achieved cryonic preservation as an evolutionary response to a harsh winter climate?

Organisms of the temperate and polar zones face tremendous challenges imposed by a seasonal climate that includes subfreezing temperatures in winter. Amphibians are unlikely candidates to have solved this challenge by allowing their bodies to partially freeze. Aside from their aforementioned complex organ and tissue

Figure 4.1 A Frozen Frog Wood frogs (*Rana sylvatica*) spend winters in a partially frozen state, without breathing and with no circulation or heartbeat. (Courtesy of J. M. Storey.)

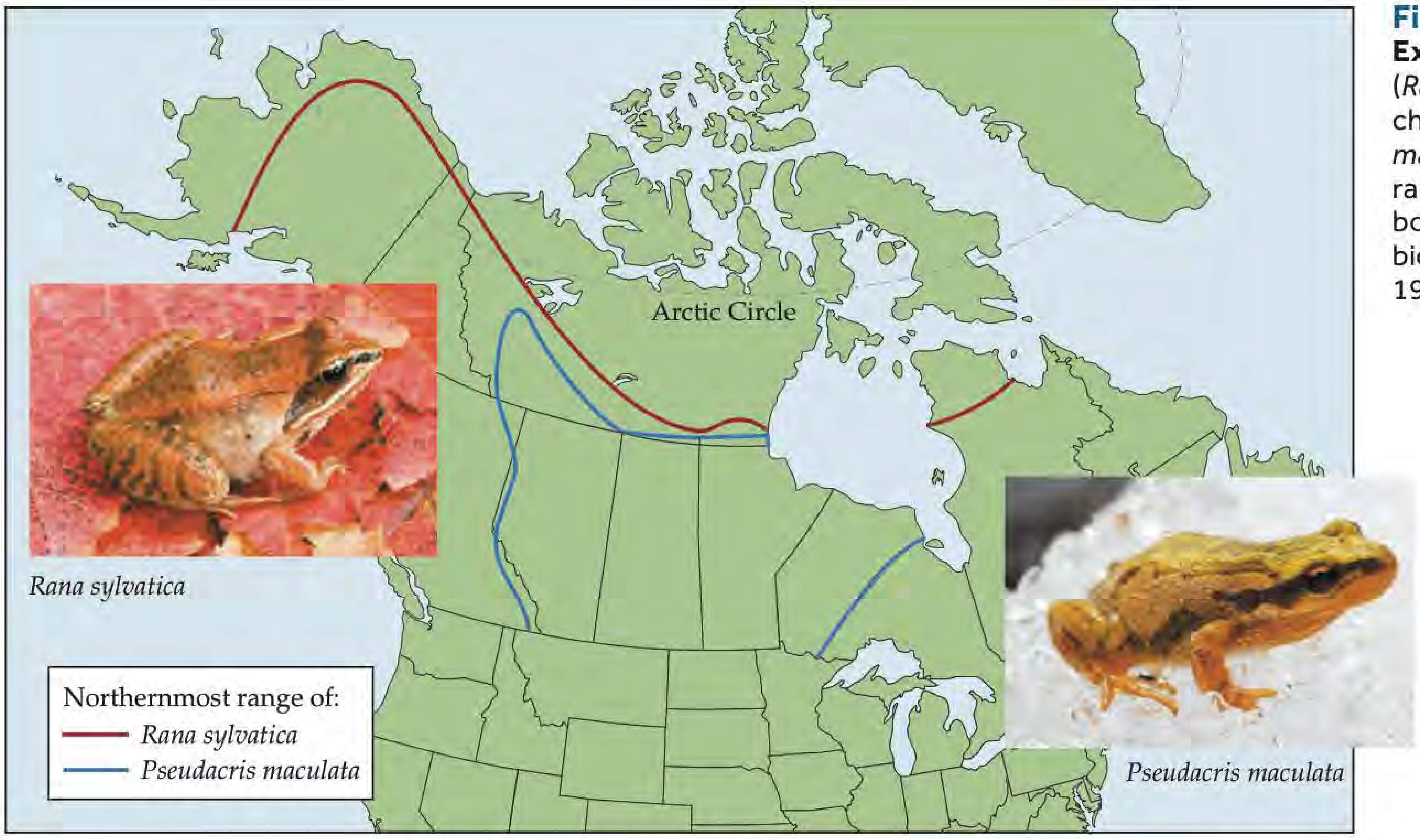


Figure 4.2 Northern Exposure Wood frogs (*Rana sylvatica*) and boreal chorus frogs (*Pseudacris maculata*) have geographic ranges that extend into the boreal forest and tundra biomes. (After Pinder et al. 1992.)

systems, amphibians are "cold-blooded" (generating little heat internally) and, as a group, first evolved in tropical and subtropical biomes. Yet two frog species, the wood frog (*Rana sylvatica*) and the boreal chorus frog (*Pseudacris maculata*), live in the tundra biome (**Figure 4.2**) (Pinder et al. 1992). These frogs survive extended periods of subfreezing air temperatures in shallow burrows in a semi-frozen state, with no heartbeat, no blood circulation, and no breathing. Among the vertebrates, only a few species of amphibians (four frogs and one salamander) and one turtle species can survive a long winter in a semi-frozen state. Freezing in most organisms results in substantial damage to tissues as ice crystals perforate cell membranes and organelles. How do these vertebrates survive being frozen without turning to mush in spring when they thaw out and reinitiate their blood circulation and breathing, like Austin Powers reemerging to take on Dr. Evil?

Introduction

Siberian spruce trees (*Picea obovata*) experience the extreme range of seasonal temperatures characteristic of a continental climate. In the Siberian boreal forest, air temperatures regularly drop below –50°C (–58°F) in winter, and in summer they reach 30°C (86°F). Being an immobile tree, the Siberian spruce lacks the option to move to Florida for the winter or head to the coast to cool off in summer. The spruce must *tolerate* these temperature extremes, surviving the 80°C (144°F) seasonal change in its body temperature. Other organisms can *avoid* these extremes through some behavior or physiological change. These two options for coping with environmental change, **tolerance** and **avoidance**, provide a useful framework for thinking about how organisms cope with the environmental extremes they face.

The range of physical environmental conditions described in Chapter 2 establishes the variation in biomes and marine biological zones described in Chapter 3. In this chapter and the next, we will examine the interactions between organisms and the physical environment that influence their survival and persistence, and therefore their geographic ranges. The study of these interactions is known as **physiological ecology**.

CONCEPT 4.1

Each species has a range of environmental tolerances that determines its potential geographic distribution.

Responses to Environmental Variation

A fundamental principle in ecology is that the geographic ranges of species are related to constraints imposed by the physical and biological environments. In this section, we will discuss the general principles of organismal responses to the physical environment.

Species distributions reflect environmental influences on energy acquisition and physiological tolerances

The potential geographic range of a species is ultimately determined by the physical environment, which influences an organism's *ecological success* (its survival and reproduction) in two important ways. First, the physical environment affects an organism's ability to obtain the energy and resources required to maintain its metabolic functions, and therefore to grow and reproduce. Rates of photosynthesis and abundances of prey, for example, are controlled by environmental conditions. Therefore, the ability of a species to maintain a viable population is constrained at the limits of its potential geographic range. Second, as we saw in Concept 2.1, an organism's survival can be affected by extreme environmental conditions. If temperature, water supply, chemical concentrations, or other physical conditions exceed what an organism can tolerate, the organism will die. These two influences—the availability of energy and resources and physical tolerance limits—are not mutually exclusive, as energy supply influences an organism's ability to tolerate environmental extremes. Furthermore, it is important to keep in mind that the *actual* geographic distribution of a species differs from its *potential* distribution because of other factors, such as dispersal ability (see Concept 18.1), disturbance (e.g., fire; see Concept 17.1), and interactions with other organisms, such as competition (see Unit 4) (**Figure 4.3**).

As we saw in Concept 3.1, the immobility of plants makes them good indicators of the physical environment. Farmers are acutely aware of the effects of extreme events on the survival of crop plants, which are often grown outside the geographic ranges where they evolved. Frosts or extreme droughts can result in catastrophic crop losses. The aspen (*Populus tremuloides*) provides a good example of a native species whose geographic range is related to its climate tolerance. Aspen occurs in boreal forests and mountain zones throughout North America. Its geographic distribution can be predicted fairly accurately from the observed effects of climate on its survival and reproduction (Morin et al. 2007) (**Figure 4.4A**). The climate factors that limit its distribution include the effects of low temperatures on its reproductive success and the effects of drought and low temperatures on its survival (**Figure 4.4B**). The range of climate conditions under which a species occurs—its **climate envelope**—provides a useful tool for predicting its response to climate change (see Chapter 25).

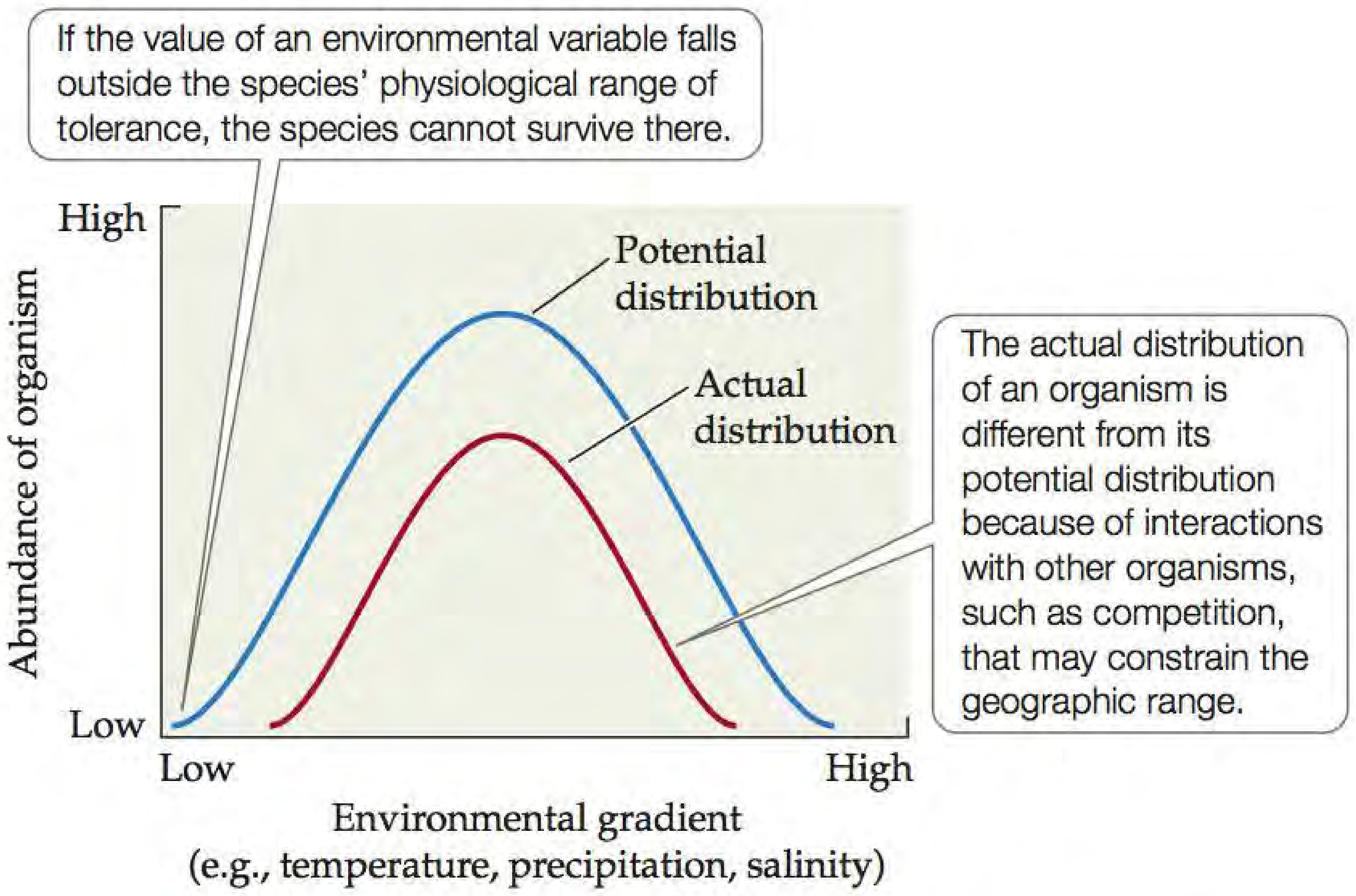


Figure 4.3 Abundance Varies across Environmental Gradients The abundance of an organism reaches a theoretical maximum at some optimal value across an environmental gradient and drops off at either end at values that constrain the potential geographic distribution of the organism. The actual abundance curve is likely to differ from the potential abundance curve because of biological interactions.

Individuals respond to environmental variation through acclimatization

Any physiological process, such as growth or photosynthesis, has a set of optimal environmental conditions most conducive to its functioning. Deviations from those optimal conditions cause a decrease in the rate of the process (**Figure 4.5**). **Stress** is the condition in which an environmental change results in a decrease in the rate of an important physiological process, thereby lowering the potential for an organism's survival, growth, or reproduction. For example, when you travel to high elevations, typically above 2,400 m (8,000 feet), the lower partial pressure of oxygen in the atmosphere (see p. 70) results in the delivery of less oxygen to your tissues by your circulatory system. This condition, known as *hypoxia*, results when the amount of oxygen picked up by hemoglobin molecules in your blood decreases. Hypoxia causes "altitude sickness," a type of physiological stress, decreasing your ability to exercise and think clearly and making you feel nauseated.

Many organisms have the ability to adjust their physiology, morphology, or behavior to lessen the effect of an environmental change and minimize the associated stress. This kind of adjustment, known as **acclimatization**,[1] is usually a short-term, reversible process. Your body acclimatizes to a high elevation if you remain there for several weeks (but only below 5,500 m, or 18,000 feet). Acclimatization to high elevations involves higher breathing rates, greater production of red blood cells and associated hemoglobin, and higher pressure in the pulmonary arteries to circulate blood into areas of the lung that are not used at lower elevations (Hochochka and Somero 2002). The outcome of these physiological changes is the delivery of more oxygen to your tissues. The acclimatization process reverses when you return to lower elevations.

Populations respond to environmental variation through adaptation

Within the geographic range of a species, particular populations occur in unique environments (e.g., cool climates,

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[1] Animal physiologists use the term "acclimatization" to refer to the short-term response of an animal to changes in the physical environment under field conditions and use "acclimation" to refer to a short-term response under controlled laboratory conditions.

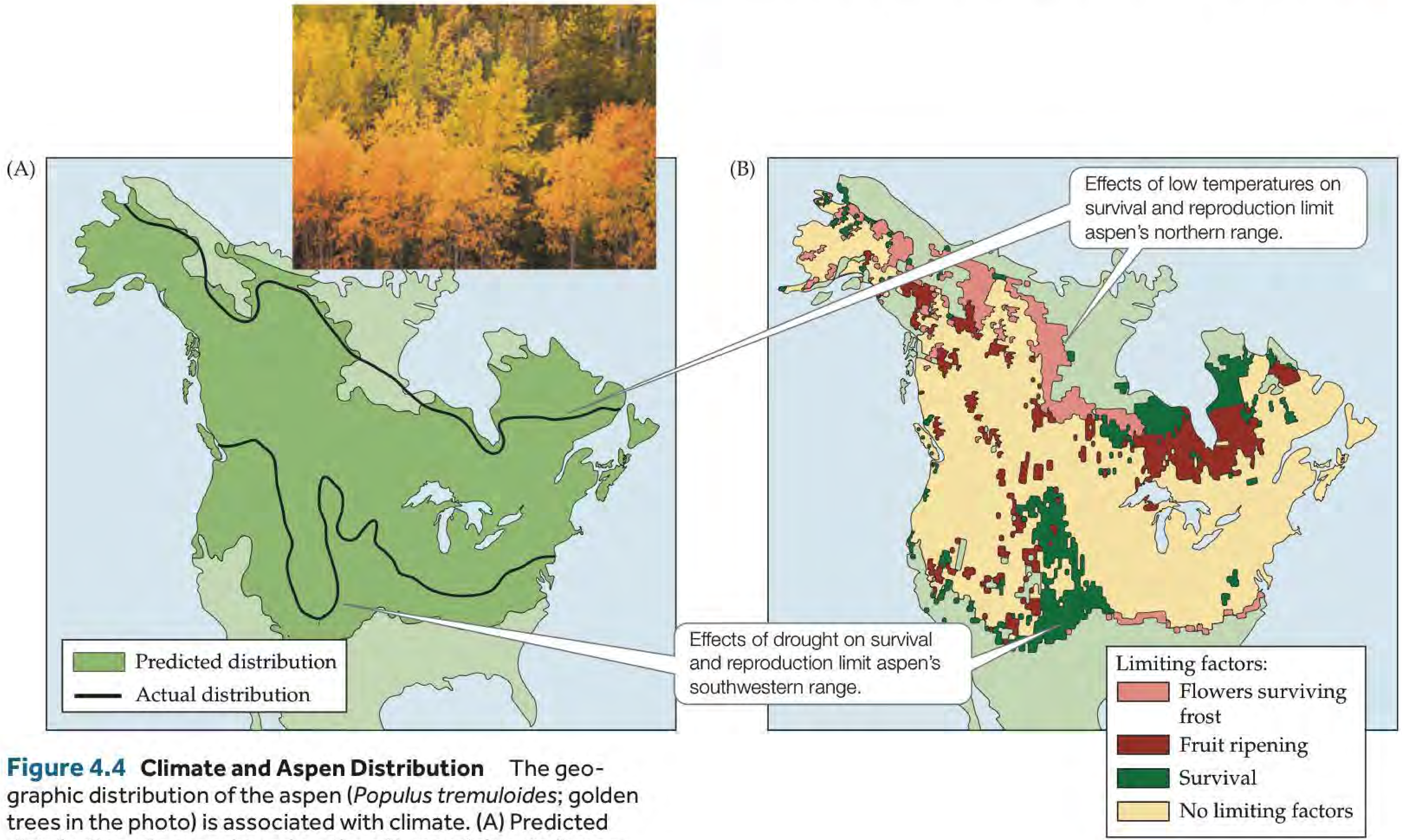


Figure 4.4 Climate and Aspen Distribution The geographic distribution of the aspen (*Populus tremuloides*; golden trees in the photo) is associated with climate. (A) Predicted distribution of aspen, based on the effects of climate factors on survival and reproduction observed in natural populations, mapped with the actual distribution. (B) Climate factors limiting the distribution of aspen, based on observations of natural populations. (After Morin et al. 2007.)

? The future climate is predicted to be warmer throughout the interior of western North America and drier in the central portions of the continent. How will these changes influence the geographic distribution of aspen?

saline soils) that may have initially been stressful to the organisms when they first occupied them. Genetic variation among the individuals within such populations in physiological, morphological, or behavioral traits that influenced their survival and functioning in the new environment would have led to natural selection favoring those individuals whose traits made them best able to cope with the new conditions. The underlying genetic basis for these traits would have resulted in a change over generations in the genetic makeup of the population as the abundance of individuals with the favored traits increased (see Concept 6.3). Such traits are known as **adaptations**. Over many generations, these unique, genetically based solutions to environmental stress would have become more frequent in the population.

Adaptation is similar to acclimatization in that both processes involve a change that minimizes stress, and the ability to acclimatize represents a type of adaptation. However, adaptation differs from acclimatization in being a long-term, genetic response of a population to environmental stress that increases its ecological success under the stressful conditions (**Figure 4.6**). Populations with adaptations to unique environments are called **ecotypes**. Ecotypes may represent responses to both abiotic (e.g., temperature, water availability, soil type, salinity) and biotic (e.g., competition, predation) environmental factors. Ecotypes can eventually become separate species as the physiology and morphology of individuals in different

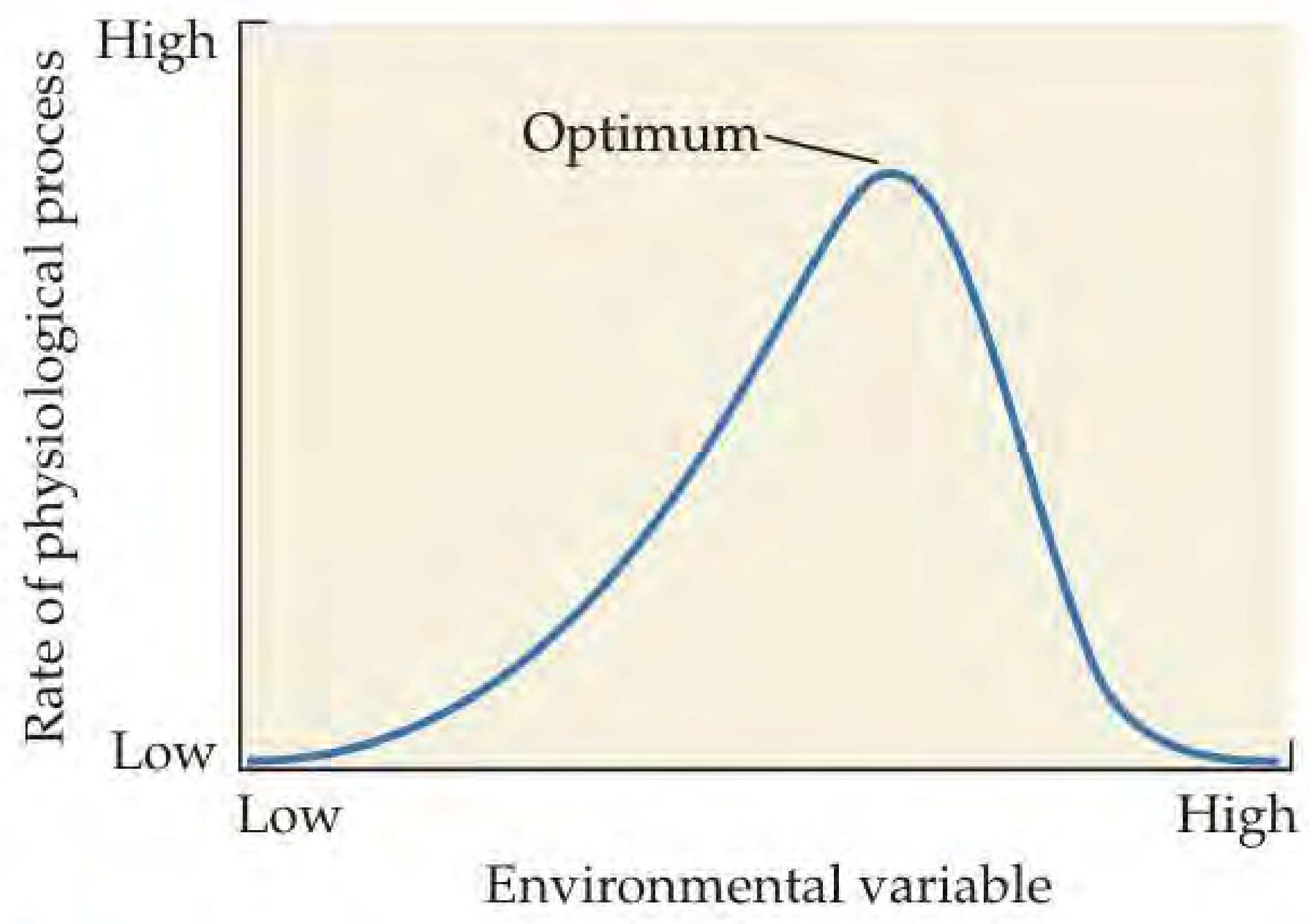


Figure 4.5 Environmental Control of Physiological Processes The rates of physiological processes are greatest under a set of optimal environmental conditions (e.g., optimal temperature, optimal water availability). Deviations from the optimum cause a decrease in the rates of physiological processes.

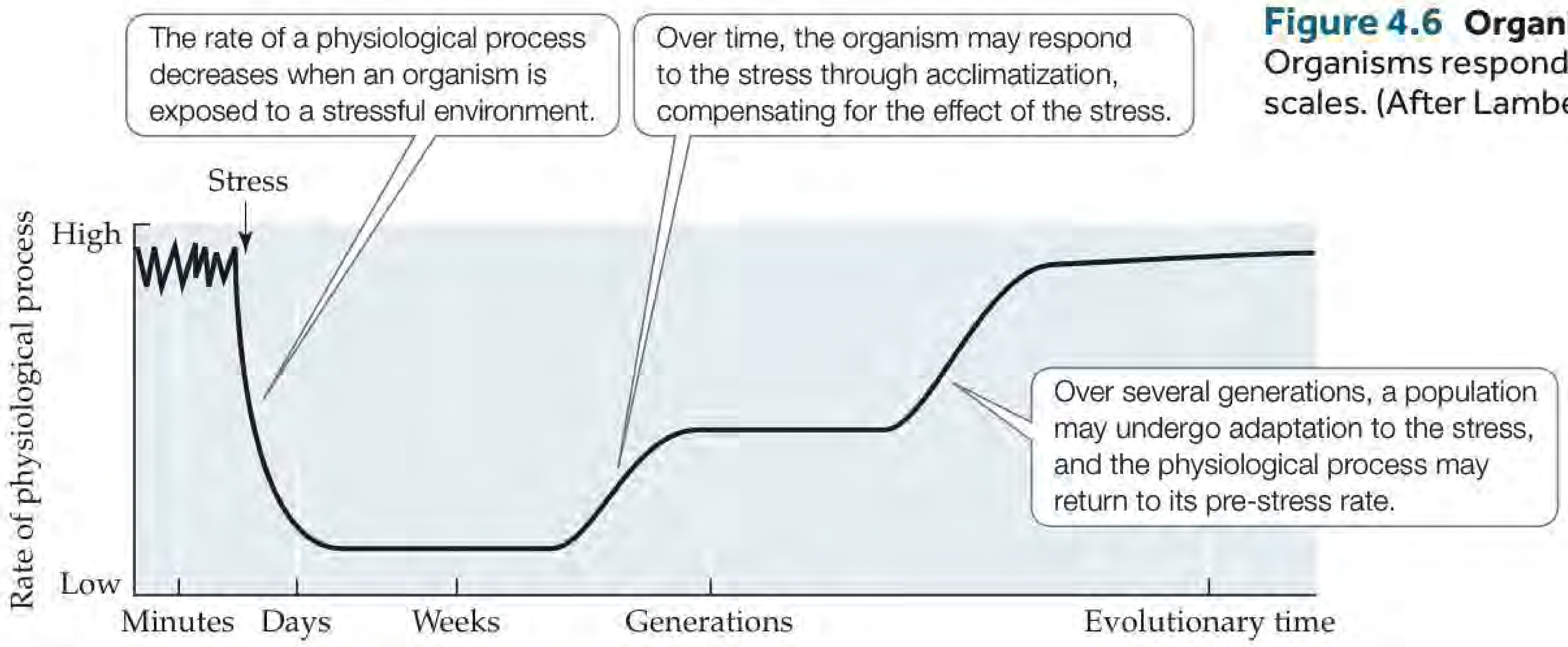


Figure 4.6 Organismal Responses to Stress Organisms respond to stress over different time scales. (After Lambers et al. 1998.)

populations diverge and the populations eventually become reproductively isolated.

Returning to our previous example of stress at high elevations, some human populations have lived continuously in the Andean highlands for at least 10,000 years. When Spanish explorers first settled in the Andes alongside the native people in the sixteenth and seventeenth centuries, their birth rates were lower than those of the natives for two to three generations, probably because of poor oxygen supply to developing fetuses (Ward et al. 1995). The same held true for the domesticated animals they brought with them. This comparison provides anecdotal evidence that the native Andean populations had become adapted to the low-oxygen conditions at high elevations. Research in the twentieth century showed that adaptations to high elevations by Andean natives include higher red blood cell production and greater lung capacity (Ward et al. 1995).

Adaptations to environmental stress can vary among populations. In other words, the solution to a particular environmental problem may not be the same for each population, as demonstrated by a comparison of human populations native to the Andean and Tibetan highlands. The adaptations to high elevations in Andean populations (high red blood cell concentration and large lung capacity) are not the same as those found in Tibetan populations (Beall 2007). Tibetan populations have red blood cell concentrations similar to and blood oxygen concentrations lower than populations at sea level, but they have a higher breathing rate, which enhances the exchange of oxygen with the blood system, and higher blood flows, which enhance delivery of oxygen to vital organs such as the brain. Thus, there are at least two different ways in which human populations have adapted to the hypoxic stress imposed by living at high elevations.

Acclimatization and adaptation are not "free"; they require an investment of energy and resources by the organism (as in the maxim "There is no free lunch" presented in Table 1.1). They represent possible *trade-offs* with other functions of the organism that may also affect its survival and reproduction. Acclimatization and adaptation must therefore increase the survival and reproductive success of the organism under the specific environmental conditions in order to be favored over other patterns of energy and resource investment. Trade-offs in energy and resource allocation are discussed in Concept 7.3.

In the remaining two sections, we will examine the factors that determine organisms' temperatures, water content, and water uptake, and we will consider examples of acclimatization and adaptation that allow organisms to function in the face of varying temperatures and water availability.

CONCEPT 4.2

The temperature of an organism is determined by exchanges of energy with the external environment.

Variation in Temperature

Environmental temperatures vary greatly throughout the biosphere, as we saw in Chapter 2. The Siberian boreal forest described earlier in this chapter represents one extreme of seasonal variation, with as much as an 80°C (144°F) swing from summer to winter. Tropical forests, on the other hand, experience far less seasonal variation in temperature, about 15°C (22°F). Soil environments, which are home to many species of microorganisms, plant roots, and animals, are buffered from aboveground environmental temperature extremes, although soil surface temperatures may change as much as or more than air temperatures. Aquatic environments also experience temperature changes over seasonal and daily time scales. Open ocean environments tend to have very little temporal variation in temperature, because of the ocean's massive volume and heat capacity. In contrast, tide pools experience large variations in water temperature as the tides rise and fall, with as much as a 20°C (36°F) change over a 5-hour period.

The survival and functioning of organisms are strongly tied to their internal temperatures. The extreme upper limit for metabolically active multicellular plants and animals is about 50°C (122°F) (**Figure 4.7**). Some archaea and bacteria that live in hot springs can function at 90°C (194°F) (Willmer et al. 2005). The extreme lower limit for organismal function is tied to the temperature at which water in cells freezes, typically between –2°C and –5°C (28°F–23°F). Some organisms can survive periods of extreme heat or cold by entering a state of **dormancy**, in which little or no metabolic activity occurs.

The internal temperature of an organism is determined by the balance between the energy it gains from and the energy it loses to the external environment. Thus, organisms must either tolerate changes in their internal temperature as the temperature of the external environment changes or modify their internal temperature by using some physiological, morphological, or behavioral means of adjusting these gains and losses. Environmental temperatures—particularly their extremes—are therefore important determinants of the distributions of organisms, as demonstrated by the relationship between biomes and global climate patterns discussed in Chapters 2 and 3.

Temperature controls physiological activity

Key biochemical reactions important to maintenance of life are temperature-sensitive. Each reaction has an optimal temperature that is related to the activity of *enzymes*, protein-based molecules that catalyze biochemical reactions. Enzymes are structurally stable under a limited range of temperatures. At high temperatures, the constituent proteins lose their structural integrity, or become *denatured*, as their bonds break. Most enzymes become denatured at temperatures between 40°C and 70°C (104°F–158°F), but enzymes in bacteria inhabiting hot springs can remain stable at temperatures up to 100°C (212°F). The upper lethal temperature for most organisms is lower than the temperature at which their enzymes become denatured because metabolic coordination among biochemical

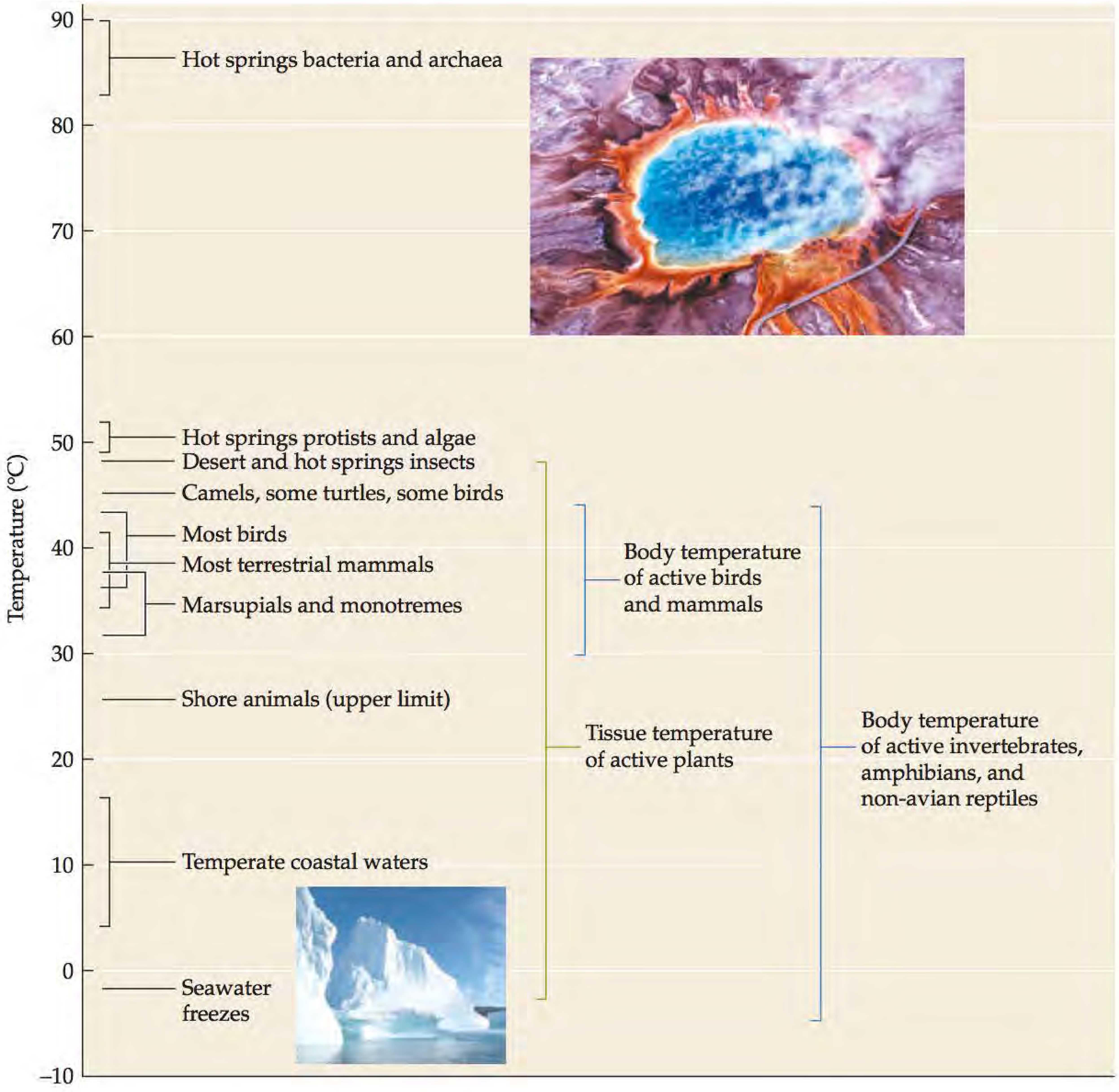


Figure 4.7 Temperature Ranges for Life on Earth Living organisms are known to exist in extreme environments, ranging from hot springs to freezing seas.

pathways is lost at these temperatures. The extreme lower limit for enzyme activity is about –5°C (23°F) (Willmer et al. 2005). The internal temperatures of Antarctic fishes and crustaceans may reach –2°C (28°F) because the salt concentration of the seawater in which they live lowers its freezing point. Some soil microorganisms are active at temperatures as low as –5°C (23°F).

Some species can produce different forms of enzymes (called *isozymes*) with different temperature optima as a means of acclimatization to changes in environmental temperature. For example, some fishes (e.g., trout, carp, goldfish) and trees (e.g., loblolly pine) can produce isozymes in response to seasonal changes in temperature. However, acclimatization to temperature changes using isozymes does not appear to be a common response in animals (Willmer et al. 2005).

Temperature also determines the rates of physiological processes by influencing the properties of membranes, particularly at low temperatures. Cell and organelle membranes are composed of two layers of lipid molecules. At low temperatures, these layers can solidify; proteins and enzymes embedded in them can lose their function, affecting processes such as mitochondrial respiration and photosynthesis, and membranes can lose their function as filters, leaking cellular metabolites. Tropical plants may suffer loss of function associated with membrane disruption at temperatures as high as 10°C (50°F), while alpine plants can function at temperatures close to freezing. The sensitivity of membrane function to low temperatures is related to the chemical composition of the membrane lipid molecules. Plants of cooler climates have a higher proportion of unsaturated membrane lipids (with greater numbers of double bonds between carbon molecules) than plants of warmer climates.

Finally, temperature influences physiological processes in terrestrial organisms by affecting water availability. As we saw in Concept 2.2, the warmer the air, the more water vapor it can hold. As a result, the rate at which terrestrial organisms lose water from their bodies increases as temperature becomes warmer. We will return to this point later when we discuss how organisms cope with variations in water availability.

Organisms influence their temperature by modifying energy balance

On a hot day, jumping into a swimming pool and then sitting in the shade in a light breeze brings relief from the oppressive heat. Elephants follow a similar routine, swimming and using their trunks to spray water onto their backs. This kind of behavior facilitates heat loss in several ways. First, the contact of warm skin with cool water causes heat energy to be lost from the body through the process of *conduction*: the direct transfer of energy from warmer, more rapidly moving molecules to cooler, more slowly moving molecules. Also, when cool water and air move across the surface of a warmer body, heat energy is carried away via *convection*. In addition, the change in the state of water from liquid to vapor as it evaporates on the skin's surface absorbs body heat (*latent heat transfer*). Finally, moving into the shade lowers the amount of energy you receive from solar *radiation*.

The balance between energy input and energy output determines whether the temperature of any object will increase or decrease. Archaea, bacteria, fungi, protists, and algae cannot avoid changes in their temperature when the environmental temperature changes. They must tolerate variations in temperature through biochemical modifications. For example, when temperatures exceed their range of tolerance, microorganisms often survive as dormant spores. Plants and animals can also influence their body temperature, and therefore their physiological processes, by adjusting their exchange of energy with the environment. Both plants and animals are often able to avoid stressful internal temperatures through behavioral and morphological modifications of energy balance. Let's examine some examples.

MODIFICATION OF ENERGY BALANCE BY PLANTS Among plants, temperature stress is experienced mainly in terrestrial environments. Marine and aquatic plants usually experience temperatures within the range that is conducive to their physiological functioning, although those in nearshore habitats can experience potentially lethal temperatures. The factors involved in the energy balance of terrestrial plants are shown in **Figure 4.8**. Energy inputs that warm the plant include sunlight and infrared radiation from surrounding objects. If the ground or air is warmer than the plant, energy inputs also include conduction and convection. Losses of energy from the plant include the emission of infrared radiation to the surrounding environment and, if the ground or air is cooler than the plant, conduction and convection. Heat loss also occurs through transpiration (evaporation of water from inside the plant) and surface evaporation, collectively referred to as *evapotranspiration*.

We can put these inputs and outputs together to determine whether the temperature of the plant is changing:

$$\Delta H_{plant} = SR + IR_{in} - IR_{out} \pm H_{conv} \pm H_{cond} - H_{et} \qquad \textbf{(4.1)}$$

where ΔH_{plant} is the heat energy change of the plant (the Greek delta usually signifies "change in"), SR is solar radiation, IR_{in} is the input of infrared radiation, IR_{out} is the output of infrared radiation, H_{conv} is convective heat transfer, H_{cond} is conductive heat transfer, and H_{et} is heat transfer through evapotranspiration. A negligible loss of energy occurs as the plant uses solar radiation for photosynthesis. If the plant is warmer than the surrounding air, H_{conv} and H_{cond} are negative. If the sum of the energy inputs exceeds the sum of the outputs, ΔH_{plant} is positive, and the plant's temperature is increasing. Conversely, if

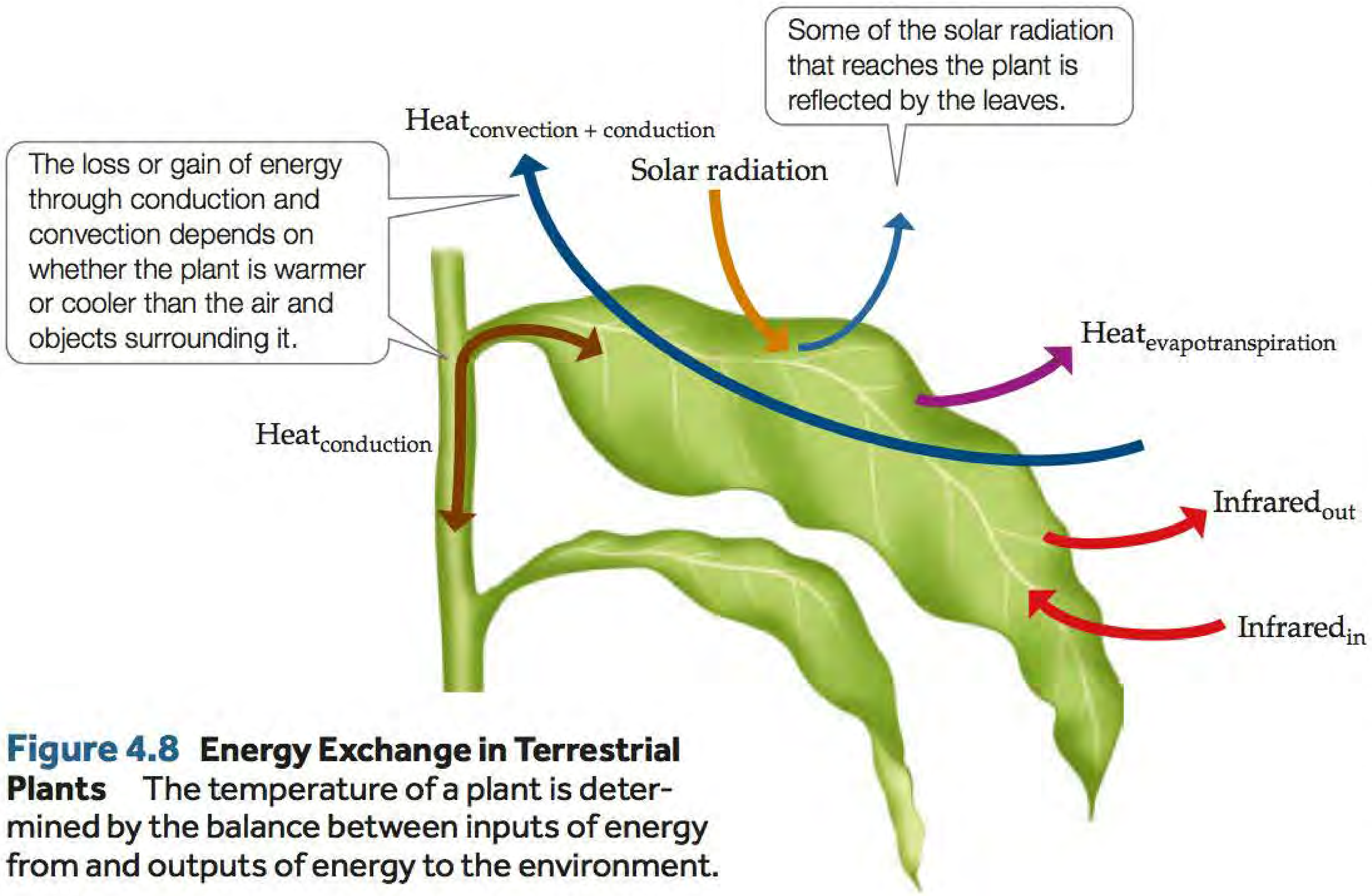


Figure 4.8 Energy Exchange in Terrestrial Plants The temperature of a plant is determined by the balance between inputs of energy from and outputs of energy to the environment.

more heat is being lost than gained, ΔH_{plant} is negative, and the plant's temperature is decreasing.

Plants can modify their energy balance to control their temperature by adjusting these energy inputs and outputs. Leaves are most often associated with these adjustments because they are the primary photosynthetic organs of the plant and typically are the most temperature-sensitive tissue. The most important and common adjustments include changes in the rate of transpirational water loss. In addition, changes in leaf surface reflective properties or in leaf orientation toward the sun can alter the amount of solar radiation absorbed by the plant. Finally, changes in convective heat transfer can be accomplished by changing surface roughness.

Transpiration is an important evaporative cooling mechanism for leaves. As we saw in Chapter 2, its effectiveness is especially evident in the canopies of tropical forests, which are subjected to warm air temperatures and high levels of solar radiation. Without transpirational cooling, the leaves of tropical canopy plants could reach temperatures over 45°C (>113°F), which would be lethal. The rate of transpiration is controlled by specialized *guard cells* surrounding pores, called **stomates**, leading to the interior of the leaf. Stomates are the gateway for both transpirational water loss and the uptake of carbon dioxide for photosynthesis; we will return to the latter function in Concept 5.2. Variation in the degree of stomatal opening, as well as in the number of stomates, controls the rate of transpiration and therefore exerts an important control on leaf temperature (**Figure 4.9**).

Transpiration requires a steady supply of water. Where the amount of water in the soil is limited—as it

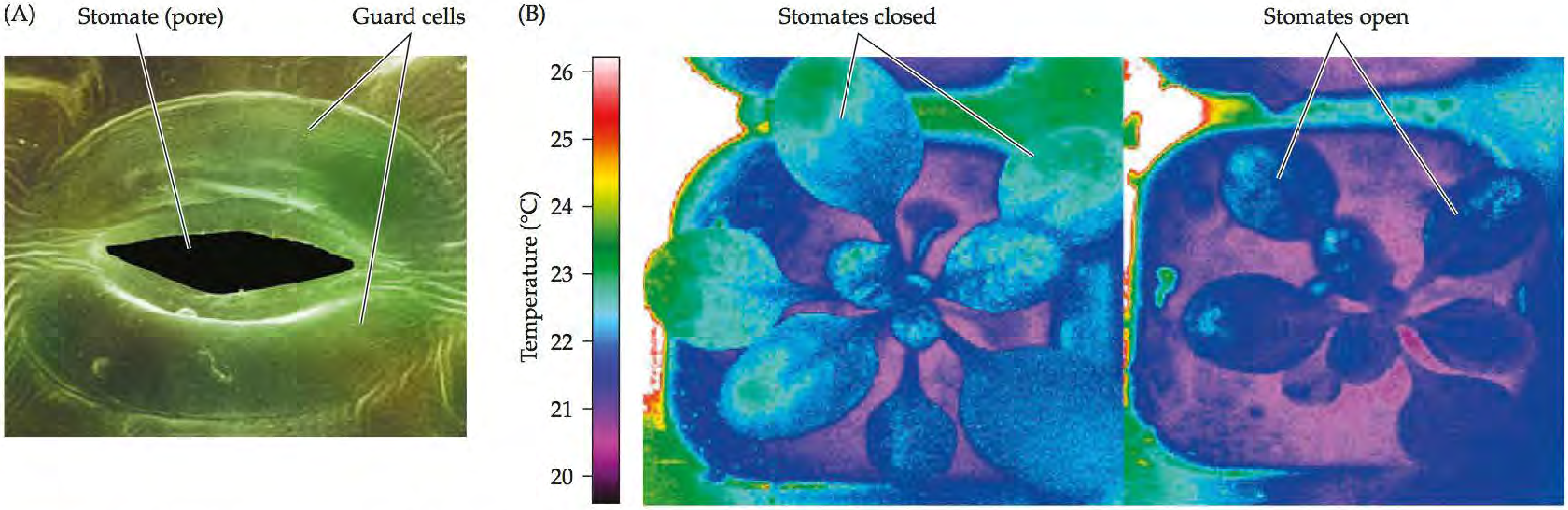


Figure 4.9 Stomates Control Leaf Temperature by Controlling Transpiration (A) Specialized guard cells control a stomate's degree of opening. Open stomates allow CO_2 to diffuse in for photosynthesis, and they allow water to transpire out, cooling the leaves. (B) Leaf temperatures vary with the degree of stomatal opening. The plant on the right has open stomates and is transpiring freely, while the plant on the left, kept under identical conditions, has closed stomates, a lower transpiration rate, and a temperature 1–2°C (2–4°F) higher, as indicated by thermal infrared imaging. (B courtesy of G. H. Holroyd and A. M. Heatherington.)

? Cooling of leaves using transpiration may be particularly important in what biomes?

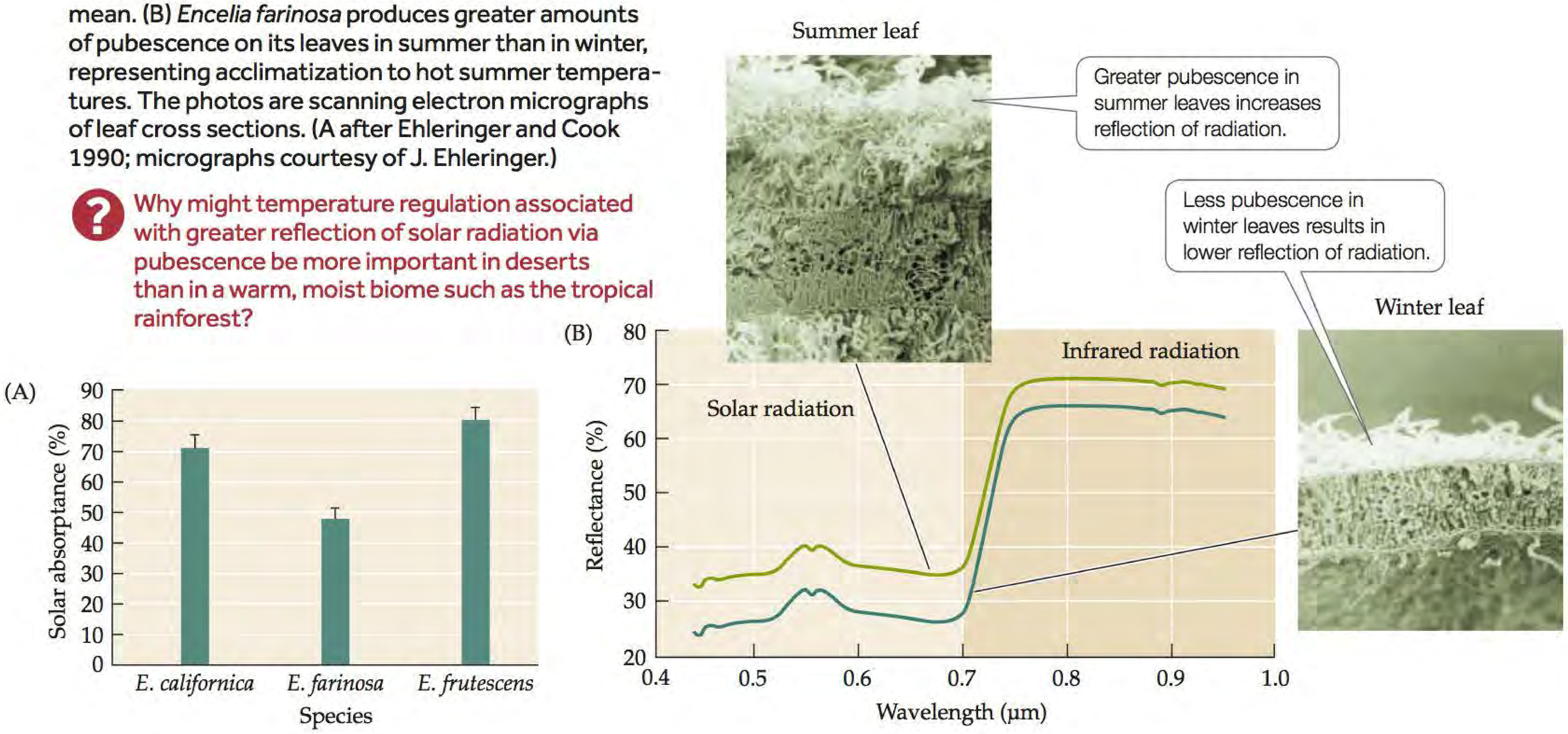
is over a substantial part of Earth's land surface—transpiration is not a reliable cooling mechanism. As we saw in Concept 3.1, some plants shed their leaves during dry seasons, thereby avoiding both temperature and water stress. However, the high demand for the resources (e.g., soil nutrients) needed to replace fallen leaves may favor protecting existing leaves rather than shedding them. Plants that maintain their leaves during long dry periods require mechanisms other than transpiration to dissipate heat energy. One option is to alter the reflective properties of leaves via **pubescence**, the presence of light-colored or white hairs on the leaf surface, which lowers the amount of solar radiation absorbed by the leaf surface. Pubescence can also lower the effectiveness of convective heat loss, however, and thus represents a trade-off between two opposing heat exchange mechanisms.

One of the best studies addressing the adaptive significance of leaf pubescence for temperature regulation has focused on shrubs of the genus *Encelia* (members of the daisy family, common name brittlebush). Jim Ehleringer and his colleagues described the role of pubescence in leaf temperature regulation among species of *Encelia* that occupy different geographic ranges. *Encelia farinosa*, a native of the Sonoran and Mojave Deserts, maintains a high amount of leaf pubescence relative to *Encelia* shrubs from moister, cooler environments. Ehleringer and his colleague Craig Cook (1990) evaluated the relative roles of leaf pubescence and transpiration in the cooling of leaves of *E. farinosa* and two other species whose leaves lack pubescence: *E. frutescens*, which occurs in desert washes (which have more moisture than the rest of the desert), and *E. californica*, native to the cooler, moister coastal sage community of California and Baja California. To control for environmental variation that could influence the morphology and physiology of the plants, they grew plants of each species from seed together in experimental plots in the Sonoran Desert and on the California coast. Half of their experimental plants were watered while the other half were left under natural conditions. They measured leaf temperatures, the degree of stomatal opening, and the amount of sunlight absorbed.

The three *Encelia* species showed few differences in leaf temperature and stomatal opening when grown in the cooler, moister California coastal garden. In the desert garden, however, *E. californica* and *E. frutescens* shed their leaves during the hot summer months under natural conditions, but *E. farinosa* did not. *Encelia frutescens* did not shed its leaves when the shrubs were watered, and its leaves maintained sublethal temperatures using transpirational cooling. *Encelia farinosa* leaves reflected about twice as much solar radiation as those of the other two species (**Figure 4.10A**), which facilitated the shrub's ability to maintain leaf temperatures lower than the air temperature.

Figure 4.10 Sunlight, Seasonal Changes, and Leaf Pubescence (A) Solar heating of leaves varies according to the amount of pubescence on those leaves. The pubescent leaves of the desert shrub *Encelia farinosa* absorb a lower percentage of the incoming solar radiation than the leaves of two nonpubescent species: *E. californica*, native to the coastal sage community of California, and *E. frutescens*, an inhabitant of moister desert wash communities. *Encelia farinosa* is therefore less dependent on transpiration for leaf cooling than the other two species. Error bars show one SE of the mean. (B) *Encelia farinosa* produces greater amounts of pubescence on its leaves in summer than in winter, representing acclimatization to hot summer temperatures. The photos are scanning electron micrographs of leaf cross sections. (A after Ehleringer and Cook 1990; micrographs courtesy of J. Ehleringer.)

? Why might temperature regulation associated with greater reflection of solar radiation via pubescence be more important in deserts than in a warm, moist biome such as the tropical rainforest?



Greater pubescence in summer leaves increases reflection of radiation.

Less pubescence in winter leaves results in lower reflection of radiation.

Ehleringer and Cook's field experiment provides correlative evidence of the adaptive value of leaf pubescence to *E. farinosa* under hot desert conditions. Additional work by Darren Sandquist and Ehleringer has supported its adaptive value, indicating that natural selection has acted on variation in pubescence among ecotypes of *E. farinosa*. Populations in drier environments have more leaf pubescence, and reflect more solar radiation, than populations from moister environments (Sandquist and Ehleringer 2003).

In addition to varying among species and populations, leaf pubescence can also vary seasonally, exemplifying acclimatization to environmental conditions. *Encelia farinosa* shrubs produce smaller, more pubescent leaves in summer and larger, less pubescent leaves in winter (**Figure 4.10B**). There are costs to being pubescent, associated with the construction of the hairs and the loss of solar radiation that could be used for photosynthesis. Thus, when temperatures are cooler or when reliable soil water is present, *E. farinosa* plants construct leaves with fewer hairs.

Heat can be lost from a leaf by convection when the air temperature is lower than the temperature of the leaf. The effectiveness of convective heat loss is related to the speed of the air moving across a surface. As the moving air experiences more friction closer to the surface of an object, the flow becomes more turbulent, forming eddies (**Figure 4.11**). This zone of turbulent flow, called the **boundary layer**, lowers convective heat loss. The thickness of the boundary layer around a leaf is related to its size and its surface roughness. Small, smooth leaves have thin boundary layers and lose heat more effectively than large or rough leaves. This relationship between the boundary layer and convective heat loss is one reason for the rarity of large leaves in desert ecosystems.

Excessive heat loss by convection can be a problem for plants (and animals) in cold, windy environments such as the alpine zone in mountains. Convection is the largest source of heat loss from the land surface in temperate alpine environments, and high winds can shred leaves in exposed sites. Most alpine plants hug the ground surface to avoid the high wind velocities. Some alpine plants produce a layer of insulating hair on their surface to lower convective heat loss. The snow lotus of the Himalayas (*Saussurea medusa*) produces a series of very densely pubescent leaves that surround the flowers of the plant (**Figure 4.12**). Although they project above the ground surface and are exposed to more wind than ground-hugging plants, the flowers of *S. medusa* remain as much as 20°C (36°F) warmer than the air by absorbing and retaining solar radiation (Tsukaya et al. 2002). The plant not only keeps its photosynthetic tissues warm, but also provides a warm environment for potential pollinators, which are in short supply in cold, windy alpine environments.

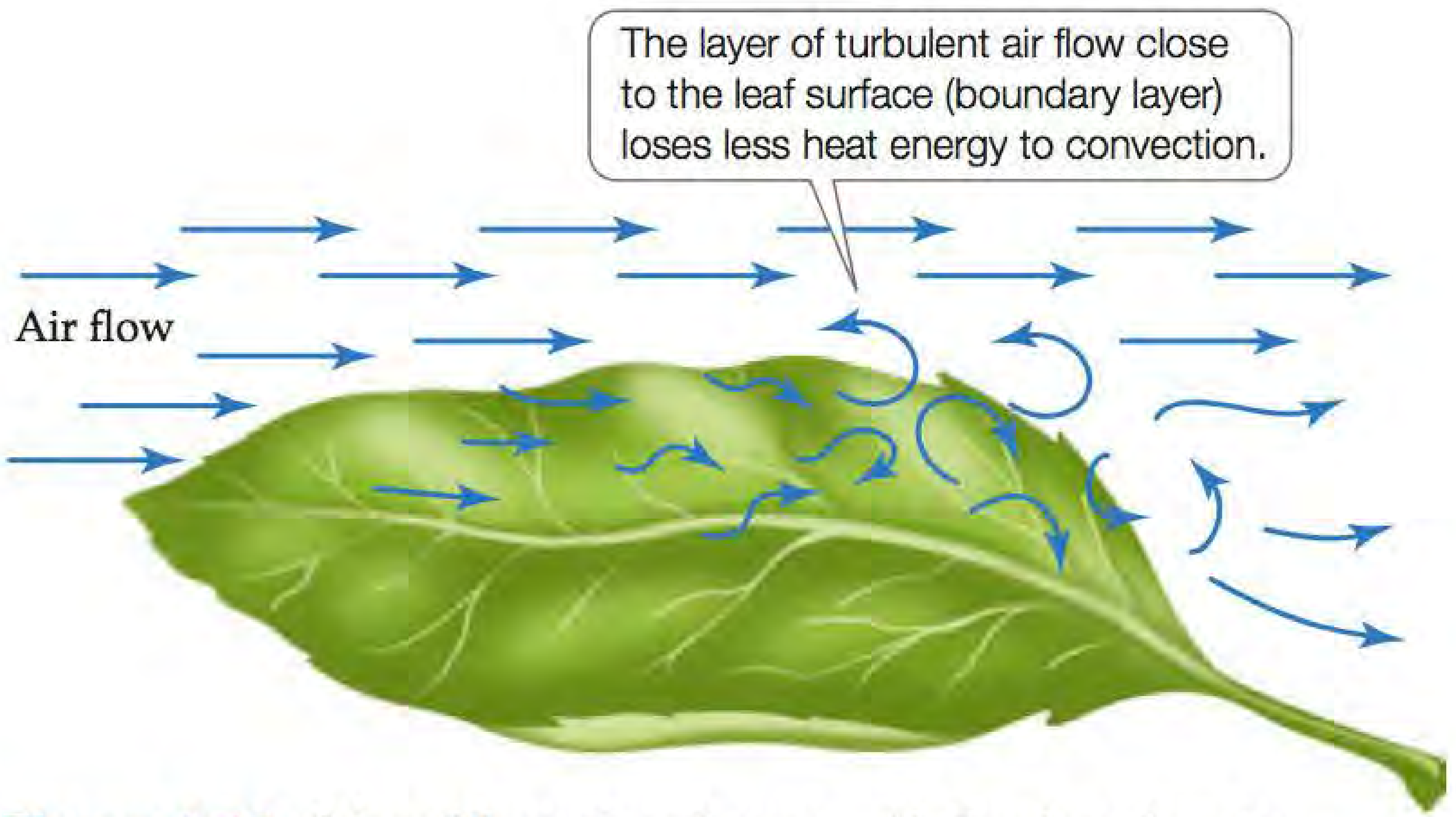


Figure 4.11 A Leaf Boundary Layer Air flowing close to the surface of a leaf is subject to friction, which causes the flow to become turbulent and lowers convective heat loss from the leaf to the surrounding air.

MODIFICATION OF ENERGY BALANCE BY ANIMALS Animals are subject to the same energy inputs and outputs described for plants in Equation 4.1, with one key difference: some animals—in particular, birds and mammals—have the ability to generate heat internally. As a result, another term is needed in the energy balance equation to represent this metabolic heat generation:

$$\Delta H_{animal} = SR + IR_{in} - IR_{out} \pm H_{conv} \pm H_{cond} - H_{evap} + H_{met} \tag{4.2}$$

where ΔH_{animal} is the heat energy change of the animal, SR is solar radiation, IR_{in} is the input of infrared radiation,

Figure 4.12 A Woolly Plant of the Himalayas The snow lotus (*Saussurea medusa*) has dense pubescence surrounding its emergent flowering stems, which provides them with thermal insulation. (Courtesy of Kenzo Okawa.)

IR_{out} is the output of infrared radiation, H_{conv} is convective heat transfer, H_{cond} is conductive heat transfer, H_{evap} is heat transfer through evaporation, and H_{met} is metabolic heat generation. In contrast to plants, evaporative heat loss is not widespread among animals. Notable examples of evaporative cooling in animals include sweating in humans, panting by dogs and other animals, and licking of the body by some marsupials under conditions of extreme heat.

The internal generation of heat by some animals represents a major ecological advance. Animals capable of metabolic heat generation can maintain relatively constant internal temperatures near the optimum for physiological functioning under a wide range of external temperatures, and as a result, they can expand their geographic ranges. Varying degrees of reliance on internal heat generation exist throughout the animal kingdom. Animals that regulate their body temperature primarily through energy exchange with the external environment, which includes the majority of animal species, are called **ectotherms**. Animals that rely primarily on internal heat generation, which are called **endotherms**, include, but are not limited to, birds and mammals. Internal heat generation is also found in some fishes (e.g., tuna), insects (e.g., bees, which generate heat for metabolic function as well as for defense; **Figure 4.13**), and even a few plant species (e.g., skunk cabbage, *Symplocarpus foetidus*, which warms its flowers using metabolically generated heat during the spring).

TEMPERATURE REGULATION AND TOLERANCE IN ECTOTHERMS Generally, ectotherms have a greater tolerance for variation in their body temperature than endotherms (see Figure 4.7), possibly because they are less able to adjust their body temperature than endotherms. The exchange of heat between an animal and the environment, whether for cooling or heating, depends on the amount of surface area relative to the volume of the animal. A larger surface area relative to volume allows greater heat exchange but makes it harder to maintain a constant internal temperature in the face of variable external temperatures. A smaller surface area relative to volume decreases the animal's ability to gain or lose heat. This relationship between surface area and volume imposes a constraint on the body size and shape of ectothermic animals. Generally speaking, the surface area-to-volume ratio decreases as body size increases, and the animal's ability to exchange heat with the environment decreases as well. As a result, large ectothermic animals are considered improbable. This conclusion has led to speculation that large dinosaurs may have had some degree of endothermy.

Small aquatic ectotherms (e.g., most invertebrates and fishes) generally remain at the same temperature as the surrounding water. Some larger aquatic animals, however, can maintain a body temperature warmer than that of the surrounding water (**Figure 4.14**). For example, skipjack tuna (*Katsuwonus pelamis*) use muscle activity, in conjunction with heat exchange between blood vessels, to maintain a body temperature as much as 14°C (25°F) warmer than the surrounding seawater. Other large oceanic fishes use similar circulatory heat exchange mechanisms to keep their muscles warm. Such mechanisms are particularly important for predatory species that depend on rapid acceleration to capture prey, which is aided by having warmer muscles.

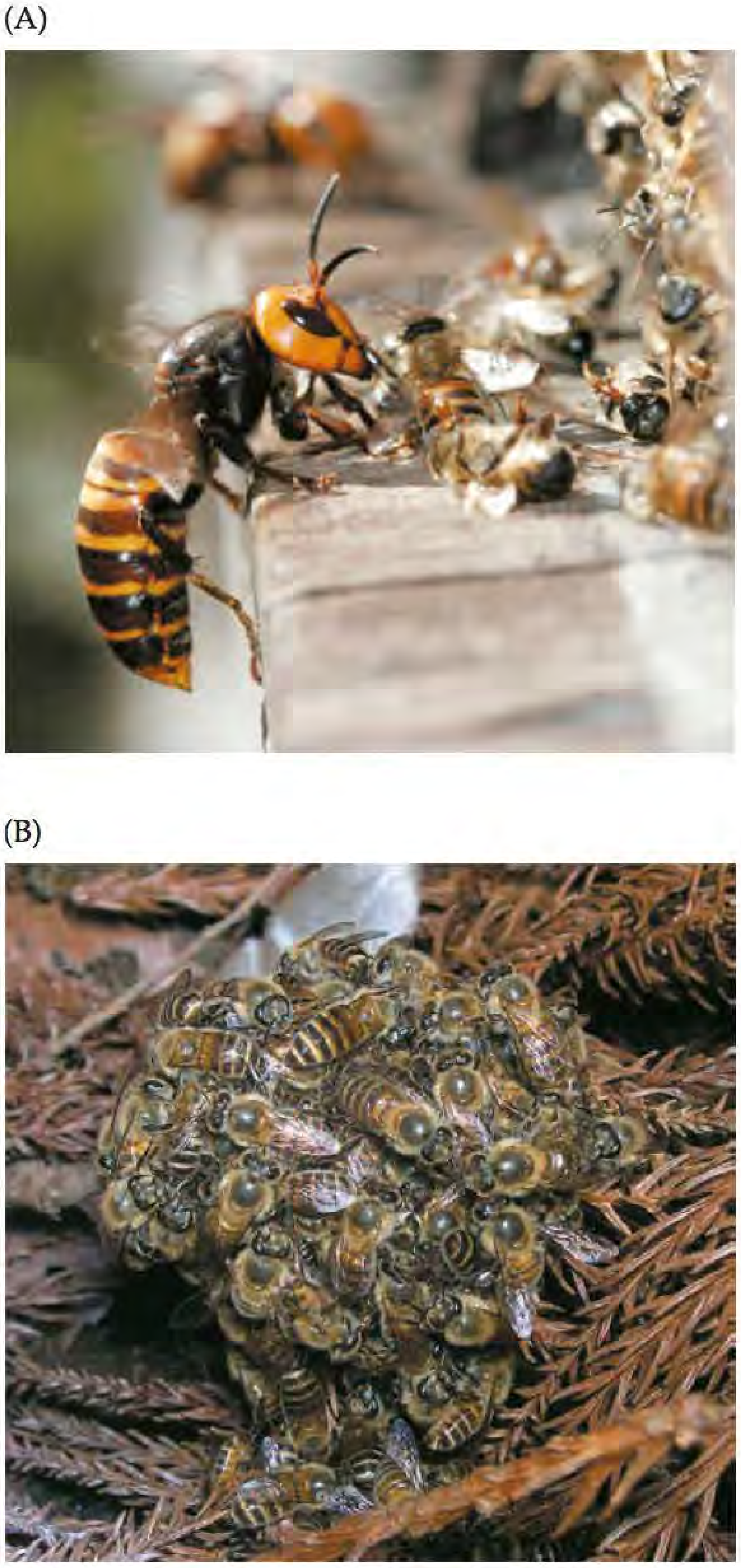


Figure 4.13 Internal Heat Generation as a Defense Bees can generate heat by contracting their flight muscles. Japanese honeybees (*Apis cerana*) use internal heat generation as a defense against Asian giant hornets (*Vespa mandarinia*) that attack bee colonies. (A) When a hornet enters a nest, the honeybees swarm the larger invader. (B) The defensive ball of bees surrounding an invading hornet generates enough heat that temperatures in the center exceed the upper lethal temperature for the hornet (about 47°C, 117°F), thus killing the invader.

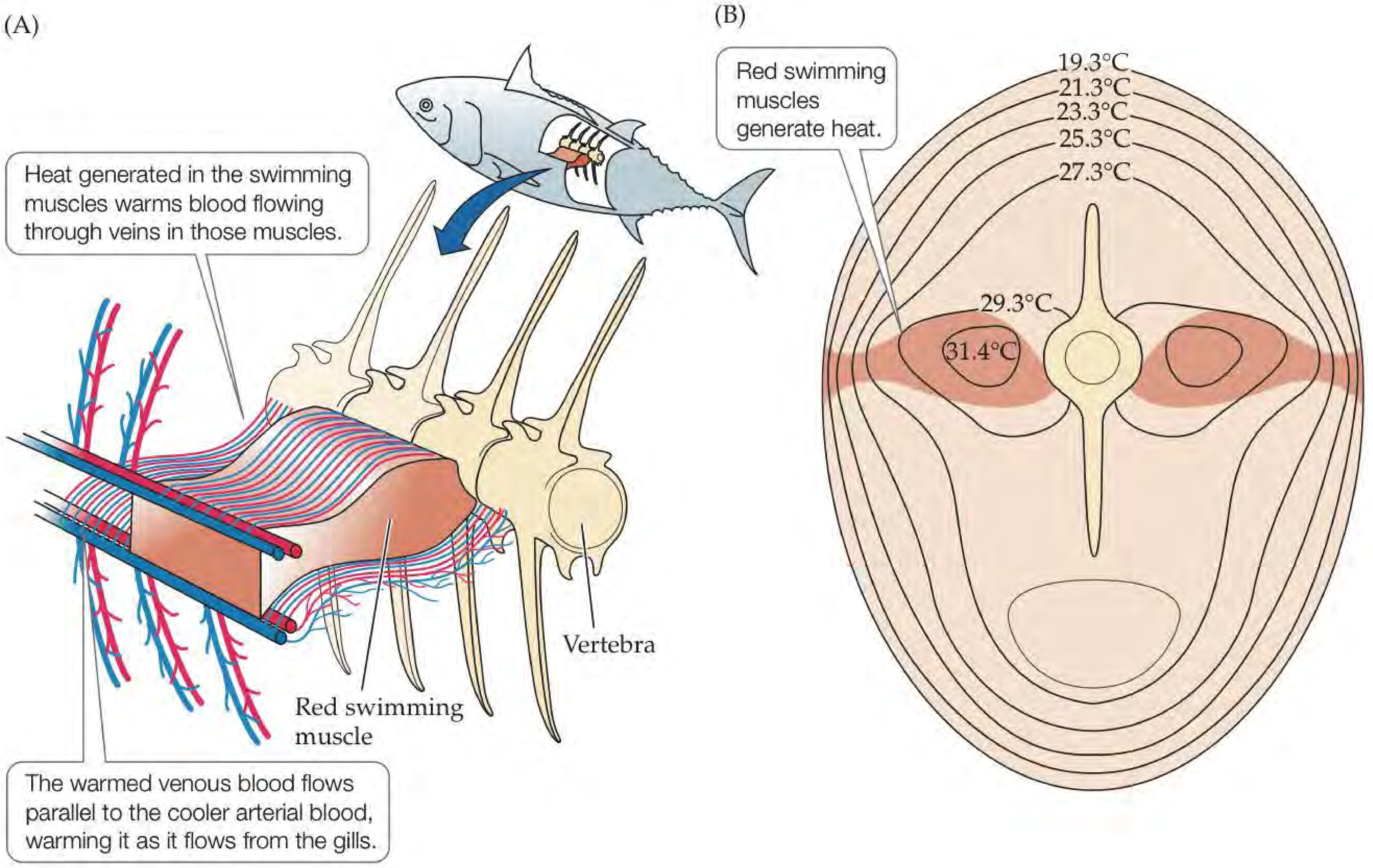


Figure 4.14 Internal Heat Generation by Tuna (A) Heat generated in the red swimming muscles of the skipjack tuna, used for cruising through the water, warms blood flowing through them, which is carried toward the body surface in veins. Those veins run parallel to arteries carrying cool oxygenated blood from the gills, warming that blood before it reaches the swimming muscles. (B) A cross section of the tuna shows that its core remains warmer than the surrounding water.

The mobility of many terrestrial ectotherms allows them to adjust their body temperature by moving to places that are warmer or cooler than they are. Basking in the sun or moving into the shade allows these animals to adjust their energy gains and losses via solar radiation, conduction, and infrared radiation. For example, reptiles and insects emerging from hiding places after a cool night will bask in the sun to warm their bodies prior to initiating their daily activities (**Figure 4.15**). This basking behavior, however, increases their risk of being found by predators. Many of these animals rely on camouflage (also called *crypsis*) to escape detection while basking. In addition to moving between locations with different temperatures, reptiles may regulate their body temperatures by altering their coloration and changing their orientation to the sun.

Because they rely on the external environment for temperature regulation, the activities of ectothermic animals are limited to certain temperature ranges. When temperatures are warm, ectotherms in sunny environments (e.g., deserts) may gain enough energy from the environment to push their body temperatures to lethal levels. **Online Climate Change Connection 4.1** describes how increases in temperature associated with climate change over the past two decades appear to have limited the daily foraging periods of several species of Mexican lizards, whose abundances have decreased significantly during this period (also see Concept 25.2).

In temperate and polar regions, temperatures drop below freezing for extended periods. Ectotherms inhabiting these regions must either avoid or tolerate exposure to subfreezing temperatures. Avoidance may take the form of seasonal migration (e.g., moving to a lower latitude) or movement to local microhabitats where temperatures stay at or above freezing (e.g., burrowing into the soil). Tolerance of subfreezing temperatures involves minimizing the damage associated with ice formation in cells and tissues. If ice forms as crystals, it will puncture cell membranes

Figure 4.15 Mobile Animals Can Use Behavior to Adjust Body Temperature This desert collared lizard (*Crotaphytus bicinctores*) has moved into a sunny location to raise its body temperature to a range suitable for undertaking its daily activities.

? What components of energy exchange are affected by this lizard's behavior?

and disrupt metabolic functioning. Some insects inhabiting cold climates contain high concentrations of glycerol, a chemical compound that minimizes the formation of ice crystals and lowers the freezing point of body fluids. These insects spend winter in a semi-frozen state, emerging in spring when temperatures are more conducive to physiological activity. Vertebrate ectotherms generally do not tolerate freezing to the degree that invertebrate ectotherms do, because of their larger size and greater physiological complexity. A very few amphibians, however, can survive being partially frozen, as described in the Case Study at the opening of this chapter.

TEMPERATURE REGULATION AND TOLERANCE IN ENDOTHERMS Endotherms tolerate a narrower range of body temperatures (30°C–45°C, 86°F–113°F) than ectotherms. However, the ability of endotherms to generate heat internally has allowed them to greatly expand their geographic ranges and the times of year they can be active. Endotherms can remain active at subfreezing environmental temperatures, something that most ectotherms cannot do. The cost of being endothermic is a high demand for food to supply energy to support metabolic heat production. The rate of metabolic activity in endotherms is associated with the external temperature and the rate of heat loss. The rate of heat loss, in turn, is related to body size because of its influence on surface area-to-volume ratio. Small endotherms have higher metabolic rates, require more energy, and have higher feeding rates than large endotherms.

Endothermic animals maintain a constant *basal* (resting) *metabolic rate* over a range of environmental temperatures known as the **thermoneutral zone**. Within the thermoneutral zone, minor behavioral or morphological adjustments are sufficient for maintaining an optimal body temperature. When the environmental temperature drops to a point at which heat loss is greater than metabolic heat production, the body temperature begins to drop, triggering an increase in metabolic heat generation. This point is called the **lower critical temperature** (**Figure 4.16A**). The thermoneutral zone and the lower critical temperature differ among mammal species (**Figure 4.16B**). As one would expect, mammals from the Arctic have lower critical temperatures below those of animals from tropical regions. Note also that the rate of metabolic activity (slope of the line) increases more rapidly below the lower critical temperature in tropical than in Arctic mammals.

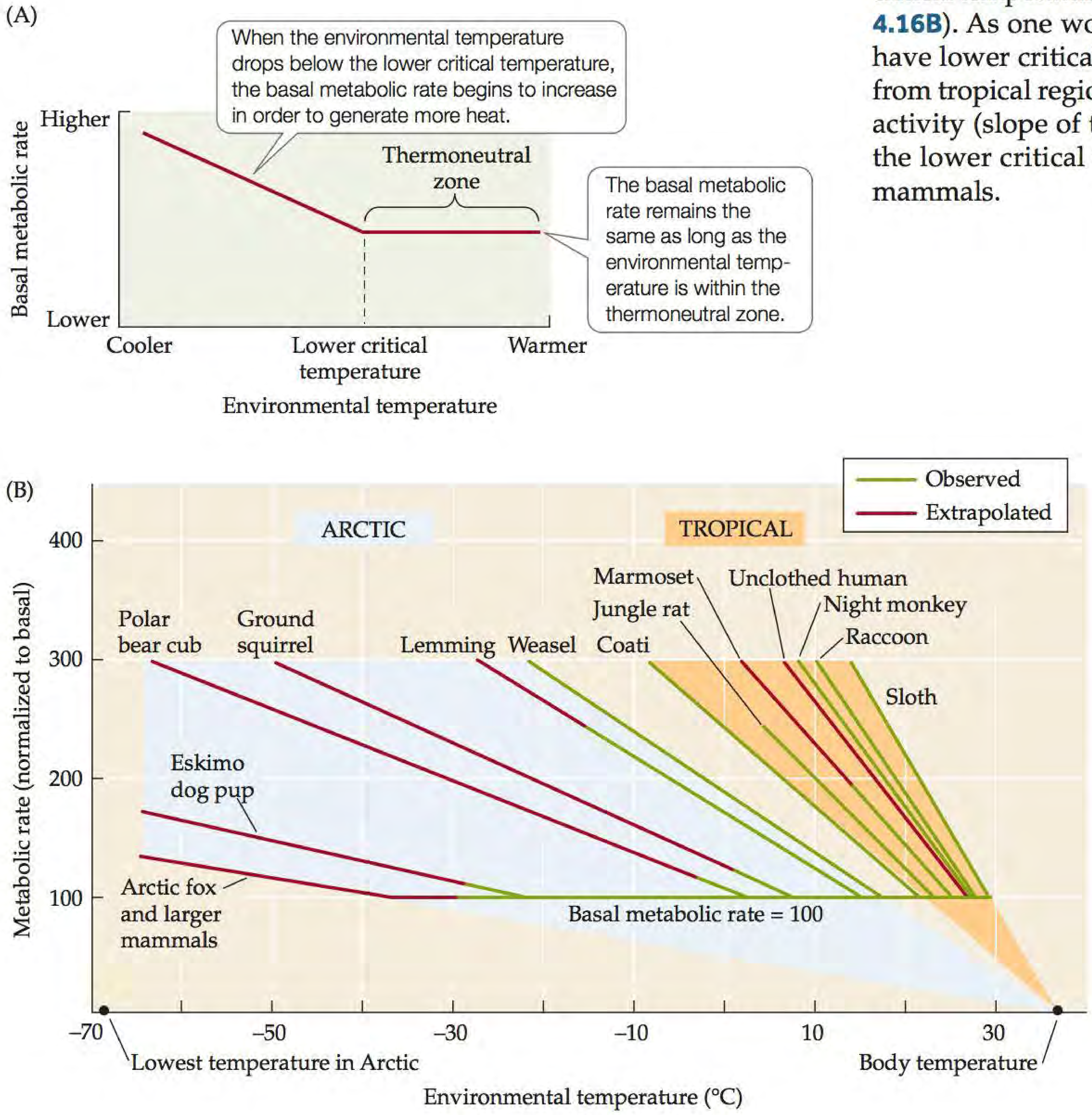


Figure 4.16 Metabolic Rates in Endotherms Vary with Environmental Temperatures (A) An endotherm's resting, or basal, metabolic rate stays constant throughout a range of environmental temperatures known as the thermoneutral zone. When environmental temperatures reach a lower limit, known as the lower critical temperature, the endotherm's metabolic rate increases to generate additional heat. (B) The thermoneutral zones and lower critical temperatures of endotherms vary with their habitats. The lower critical temperatures of Arctic endotherms are lower than those of tropical endotherms, and their metabolic rates increase more slowly below those lower critical temperatures, as shown by the shallower slopes of the curves. (After Scholander et al. 1950.)

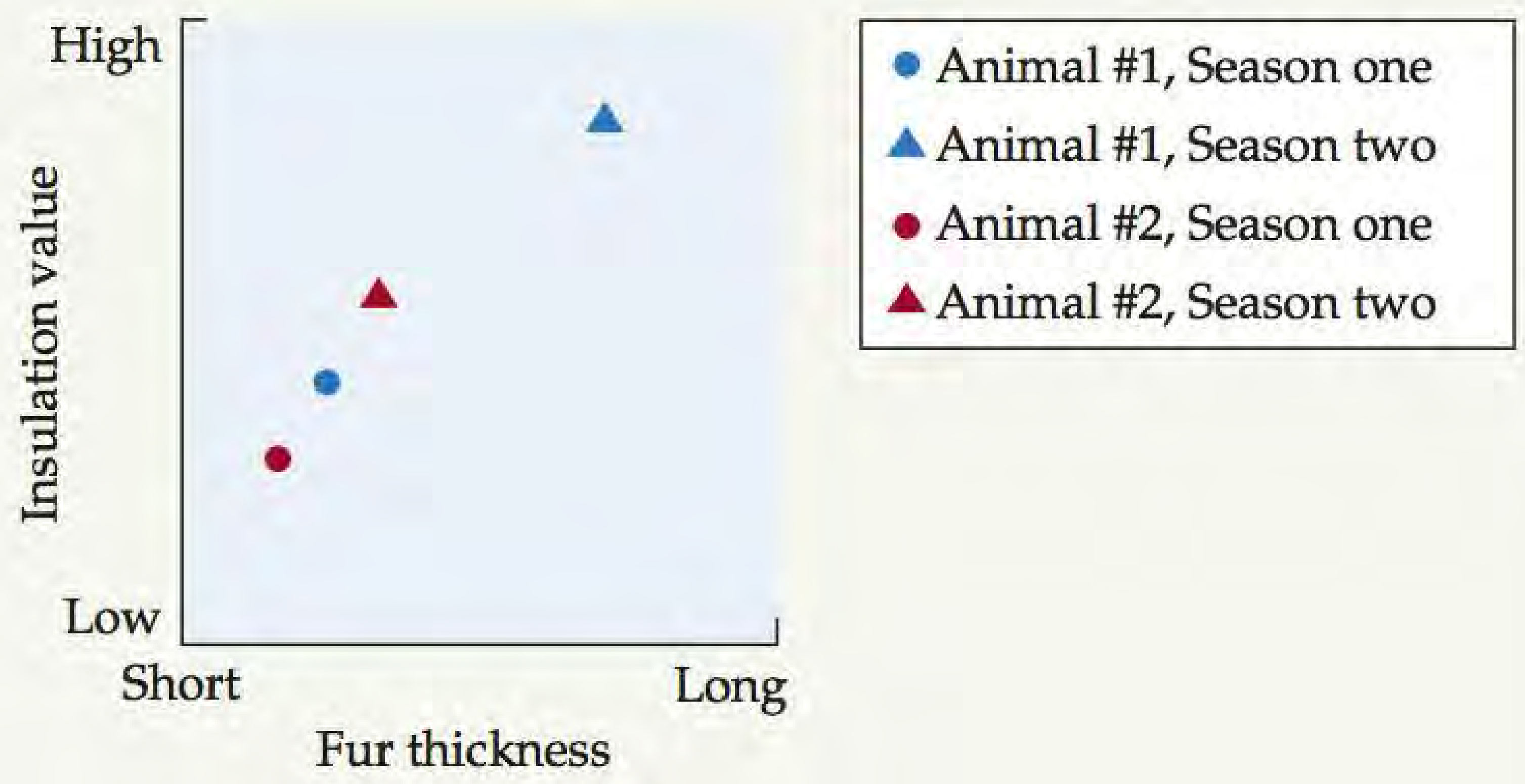
ANALYZING DATA 4.1

How Does Fur Thickness Influence Metabolic Activity in Endotherms?

Some endotherms exhibit seasonal changes in fur thickness, which helps to enhance heat loss during summer and retain heat generated by the body during winter. This seasonal change in fur thickness in individual animals is an example of acclimatization to changes in temperature.

The graph* shows the insulation value (how well heat is retained) versus fur thickness for two animals of the boreal forest biome, a red squirrel (*Tamiasciurus hudsonicus*) and a wolf (*Canis lupus*). Both animals are endotherms that exhibit acclimatization to seasonal temperature changes by changes in fur thickness.

1. Each animal is represented by a color (blue or red). Which color do you think belongs to which animal, and why?



2. Which season (summer or winter) is represented by the circles, and which by the triangles? Which animal experiences greater seasonal acclimatory changes in fur length? In what additional way might the animal with the smaller change in fur length cope with extreme winter cold?

See the companion website for a similar ANALYZING DATA exercise.

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*After P. Willmer, G. Stone and I. Johnston. 2005. *Environmental Physiology of Animals*. Blackwell Publishing, Malden, MA

What causes these differences in metabolic adjustments between endotherms of different biomes? For endothermy to work efficiently, animals must be able to retain their metabolically generated heat. Thus, the evolution of endothermy in birds and mammals required insulation: feathers, fur, or fat. These insulating layers provide a barrier limiting conductive (and in some cases, convective) heat loss. Fur and feathers insulate primarily by providing a layer of still air, similar to a boundary layer, adjacent to the skin. Differences in insulation help explain the differences among the endotherms in Figure 4.16B. Arctic mammals generally maintain thick fur. In warmer climates, however, the ability to cool off through conduction and convection is inhibited by insulation, and thick fur can be an impediment to maintaining an optimal body temperature. Some endotherms acclimatize to seasonal temperature changes by growing thicker fur in winter and shedding fur when temperatures get warmer (a fact that most pet owners know well) (**Analyzing Data 4.1**). Our human ancestors evolved in the hot tropical regions of Africa and lost much of their hairy insulating layer about 2 million years ago (Jablonski 2006).

Cold climates are tough on small endotherms. Small mammals, by necessity, have thin fur, since thick fur would inhibit their mobility. The high demand for metabolic energy below the lower critical temperature, the low insulation values of their fur, and their low capacity to store energy make small mammals improbable residents of polar, alpine, and temperate habitats. However, the faunas of many of these cold climates contain many small endotherms, sometimes in high abundances. What explains this apparent discrepancy? Small endotherms, such as rodents and hummingbirds, are able to alter their lower critical temperature during cold periods by entering a state of dormancy known as **torpor**. The body temperatures of animals in torpor may drop as much as 20°C (36°F) below their normal temperatures. The metabolic rate of an animal in torpor is 50%–90% lower than its basal metabolic rate, providing substantial energy savings (Schmidt-Nielsen 1997). However, energy is still needed to arouse the animal from torpor and bring its body temperature back up to its usual set point. Thus, the length of time an animal can remain in torpor is limited by its reserves of energy. Small endotherms may undergo *daily torpor* to minimize the energy needed during cold nights. Torpor lasting several weeks during the winter, sometimes referred to as **hibernation**, is possible only for animals that have access to enough food and can store enough energy reserves, such as marmots (**Figure 4.17**). Hibernation is somewhat rare in polar climates because few animals have access to enough food to provide enough stored energy (in the form of fat) to get through winter without eating. Some large animals, such as bears, enter a long-term winter sleep (sometimes called denning) during which the body temperature decreases only slightly, rather than going into torpor.

Just as organisms must balance energy input and output to maintain an optimal temperature, they must balance the movement of water into and out of their bodies to maintain optimal conditions for physiological functioning.

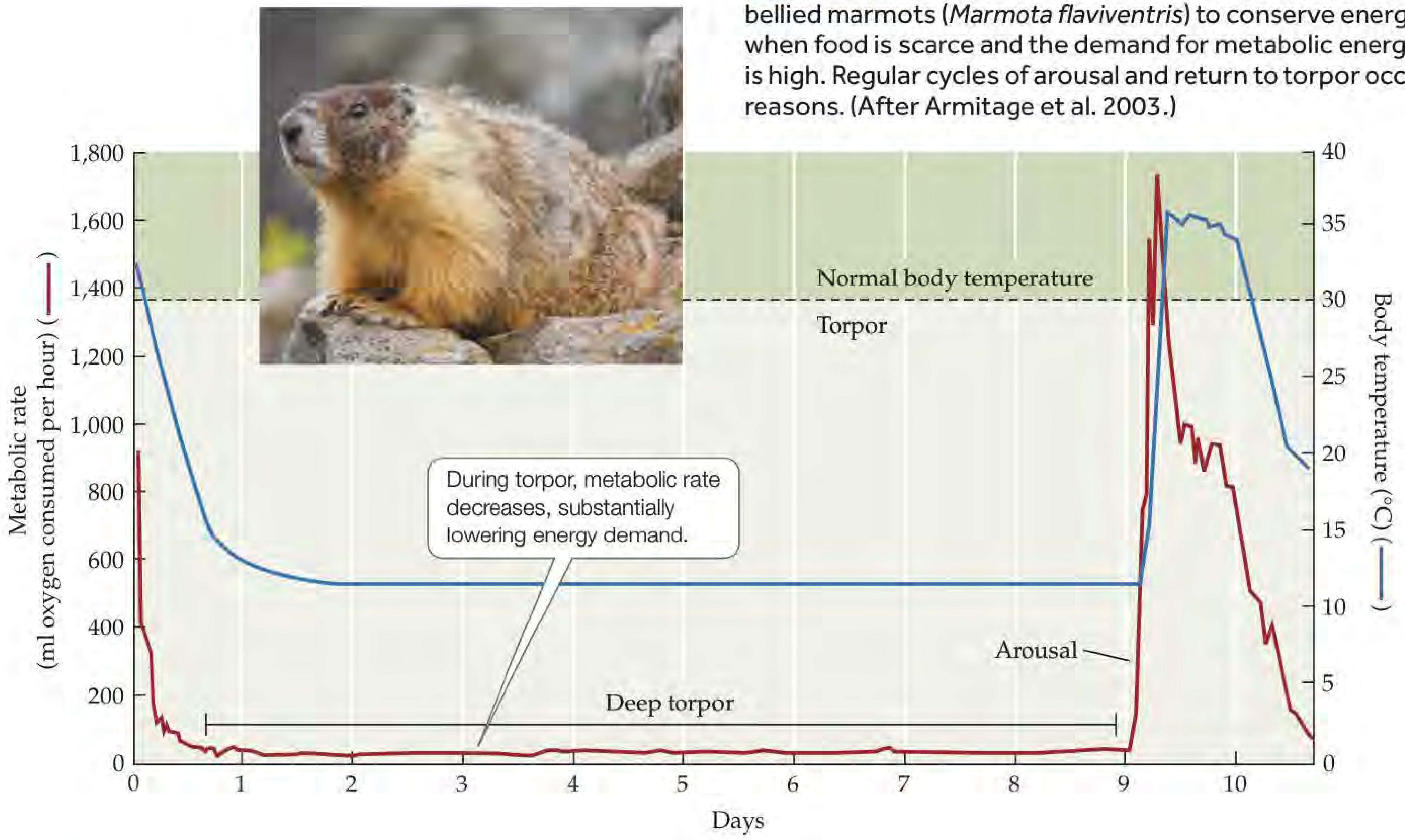

Figure 4.17 Long-Term Torpor in Marmots Torpor allows yellow-bellied marmots (*Marmota flaviventris*) to conserve energy during winter, when food is scarce and the demand for metabolic energy to keep warm is high. Regular cycles of arousal and return to torpor occur for unknown reasons. (After Armitage et al. 2003.)

CONCEPT 4.3

The water balance of an organism is determined by exchanges of water and solutes with the external environment.

Variation in Water Availability

Water is essential for life. Water is the medium in which all biochemical reactions necessary for physiological functioning occur. Water has unique properties that make it a universal solvent for biologically important *solutes* (compounds that are dissolved in water, including salts). The range of organismal water content conducive to physiological functioning is relatively narrow, between 60% and 90% of body mass. Maintaining water content within this range is a challenge primarily to organisms of freshwater and terrestrial environments. Marine organisms seldom gain or lose too much water because they exist in a medium that is conducive to maintaining water balance: the oceans in which life first evolved.

In addition to maintaining a suitable water balance, organisms must also balance the uptake and loss of solutes, primarily salts. Salt balance is closely tied to water balance because the movements of water and salts influence each other. Aquatic environments may be more saline than an organism's cells or blood (*hyperosmotic*; *hyper*, "greater"), of similar salinity (*isoosmotic*; *iso*, "same"), or less saline (*hypoosmotic*; *hypo*, "less"). Most marine invertebrates rarely face problems with water and solute balance because they tend to be isoosmotic.

Terrestrial organisms face the problem of losing water to a dry atmosphere, while freshwater organisms may lose solutes to, and gain water from, their environment. The evolution of freshwater and terrestrial organisms is very much a story of dealing with the need to maintain water balance. In this section, we will review some basic principles related to water and solute balance and provide some examples of how freshwater and terrestrial organisms maintain a water balance that is conducive to physiological functioning.

Water flows along energy gradients

Water flows along energy gradients, from high-energy to low-energy conditions. What is an energy gradient in the context of water? Gravity represents one example that is intuitively obvious: liquid water flows downhill, following a gradient of *potential energy*. Another type of energy influencing water movement is *pressure*. When elephants spray water out of their trunks, the water is flowing from a condition of higher energy inside the trunk (where muscles exert pressure on it) to a condition of lower energy outside of the trunk (where muscle pressure is not present).

Other, less obvious factors that influence the flow of water are important to organismal water balance. When solutes are dissolved in water, the solution loses energy. Thus, if the water in a cell contains more solutes than the water surrounding it, water will flow into the cell to equilibrate the energy difference. Alternatively, solutes may flow into the surrounding medium, but most biological membranes selectively block the flow of many solutes.

In biological systems, the energy associated with dissolved solutes is called **osmotic potential**. The energy associated with gravity is called **gravitational potential**, but in a biological context it is important in water movement only in very tall trees. The energy associated with the exertion of pressure is called **pressure** (or **turgor**) **potential**. Finally, the energy associated with attractive forces on the surfaces of large molecules inside cells or on the surfaces of soil particles is called **matric potential**.

The sum of these energy components within an aqueous system determines its overall water energy status, or **water potential**. The water potential of a system can be defined mathematically as

$$\Psi = \Psi_o + \Psi_p + \Psi_m \tag{4.3}$$

where Ψ is the total water potential of the system (in units of pressure; usually megapascals, MPa), Ψ_o is the osmotic potential (a negative value because it lowers the energy status of the water), Ψ_p is the pressure potential (a positive value if pressure is exerted on the system; a negative value if the system is under tension), and Ψ_m is the matric potential (a negative value). Water will always move from a system of higher Ψ to a system of lower Ψ, following the energy gradient. This terminology is most often used in plant, microbial, and soil systems, but it works in animal systems as well.

The atmosphere has a water potential that is related to humidity. From a biological perspective, air with a relative humidity of less than 98% of saturation has a very low water potential, so the gradient in water potential between most terrestrial organisms and the atmosphere is very high. Without some barrier to water movement, terrestrial organisms would lose water rapidly to the atmosphere. Any force that impedes the movement of water (or other substances, such as carbon dioxide) along an energy gradient is called **resistance**.[2] Barriers that increase organisms' resistance to water loss include the waxy cuticle of plants and insects and the skin of amphibians, reptiles, birds, and mammals.

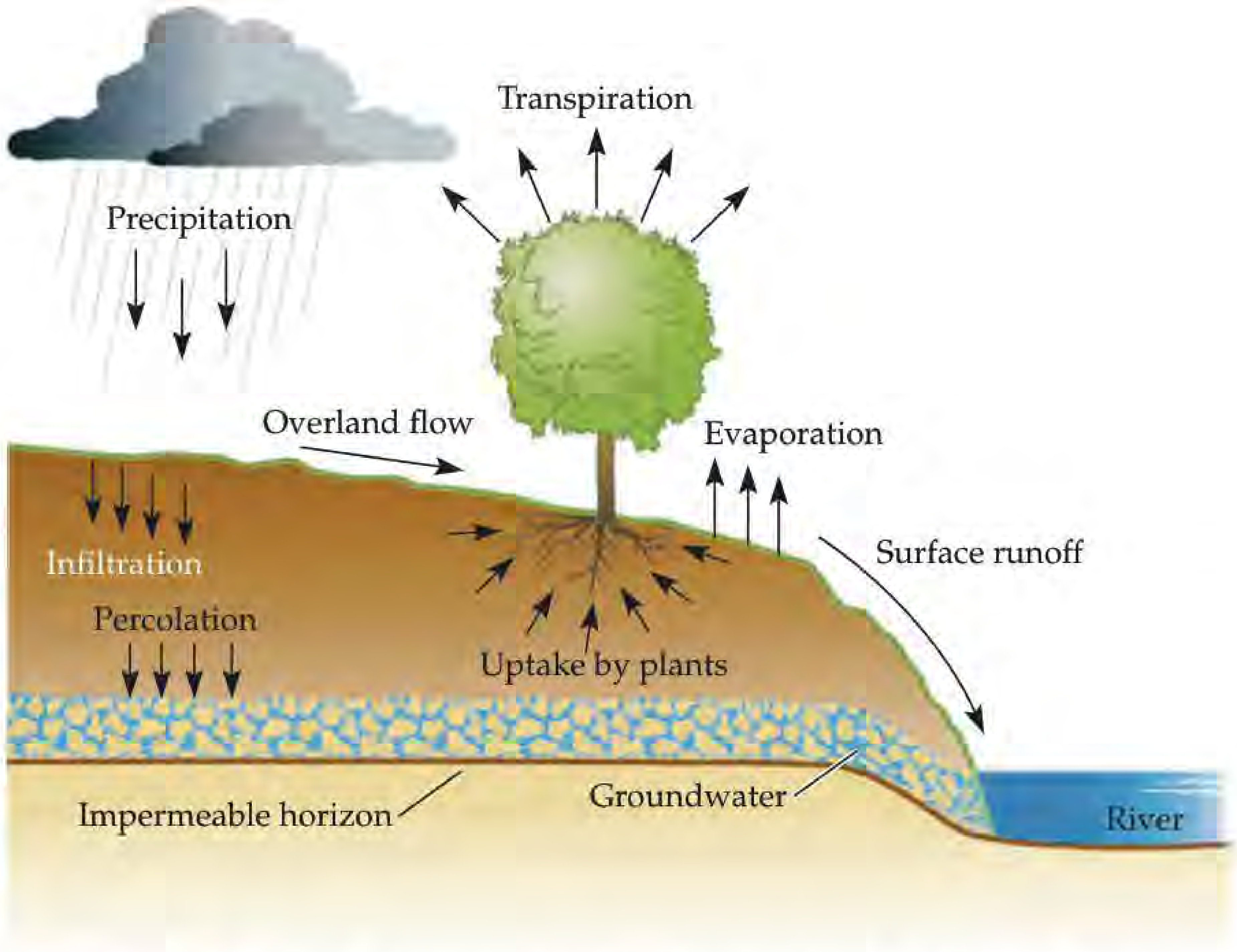

Figure 4.18 What Determines the Water Content of Soil? The water content of soil is determined by the balance between water inputs (infiltration of precipitation and overland flow of water) and outputs (percolation to deeper layers, evapotranspiration) and by the capacity of the soil to hold water. Soil water storage capacity and the rate of percolation are dependent on soil texture.

Water losses and solute gains and losses must be compensated

Terrestrial plants and soil microorganisms rely on water uptake from soils to replace the water they lose to the atmosphere. Soils are important reservoirs of water that support a multitude of ecological functions. The amount of water that soils can store is related to the balance between water inputs and outputs, soil texture, and topography (**Figure 4.18**). Water inputs include precipitation that infiltrates into the soil and overland flow of water. Water losses include percolation to deeper layers below the plant rooting zone and evapotranspiration.

The water storage capacity of most soils is dominated by their pore space and matric potential, which is related to the attractive forces on the surfaces of the soil particles. Sandy soils store less water than fine-textured soils, but fine soil particles also have a higher matric potential and thus hold onto water more tightly. Soils with mixed coarse and fine particles are generally most effective in storing water and supplying it to plants and soil organisms. When the volume of water in the soil drops below a certain point (25% of total soil mass in fine-textured soils, 5% in sandy soils), the matric forces are strong enough that most of the remaining water is unavailable to organisms. The osmotic potential of some soils also can be important, particularly where dissolved salts are found, as in soils near marine environments or where salinization (see Figure 2.28) has occurred.

WATER BALANCE IN MICROORGANISMS Single-celled microorganisms, which include archaea, bacteria, algae, and protists, are active primarily in aqueous environments. Their water balance is dependent on the water potential of the surrounding environment, which is determined mainly by its osmotic potential. In most marine and freshwater

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[2] Many physiologists prefer using conductance rather than resistance to express the influence of a barrier on the movement of water or gases between an organism and its environment. Mathematically, conductance is the reciprocal of resistance.

ecosystems, the osmotic potential of the environment changes little over time. Some environments, however, such as estuaries, tide pools, saline lakes, and soils, experience frequent changes in osmotic potential due to evaporation or variable influxes of fresh and salt water. Microorganisms in these environments must respond to these changes by altering their cellular osmotic potential if they are to maintain a water balance suitable for physiological functioning. They accomplish this through **osmotic adjustment**, an acclimatization response that involves changing their solute concentration, and thus their osmotic potential. Some microorganisms synthesize organic solutes to adjust their osmotic potential, which also help to stabilize enzymes. Others use inorganic salts from the surrounding medium for osmotic adjustment. The ability to adjust osmotic potential in response to changes in external water potential varies substantially among microorganisms: some completely lack this ability, while others (such as *Halobacterium* spp.) can adjust to even the extremely saline conditions in landlocked saline lakes.

As noted above, terrestrial environments are too dry for any organism that is unable to restrict cellular water loss to the atmosphere. Many microorganisms avoid exposure to dry conditions by forming dormant resistant spores, encasing themselves in a protective coating that prevents water loss to the environment. Some microorganisms with filamentous forms, such as fungi and yeasts, are very tolerant of low water potentials and can grow in dry environments. Most terrestrial microorganisms, however, are found in soils, which have a higher water content and humidity than the air above them.

WATER BALANCE IN PLANTS One of the distinguishing characteristics of plants is a rigid cell wall composed of cellulose. Bacteria and fungi also have cell walls, composed of materials such as chitin (in fungi) or peptidoglycans and lipopolysaccharides (in bacteria). Cell walls are important to water balance because they facilitate the development of positive **turgor pressure**. When water follows a gradient of water potential into a plant cell, it causes the cell to expand and press against the cell wall, which resists the pressure because of its rigidity (**Figure 4.19**). Turgor pressure is an important structural component of plants, and it is also an important force for growth, promoting cell division. When nonwoody plants lose turgor pressure due to dehydration, they wilt. Wilting is generally a sign that a plant is experiencing water stress.

Plants take up water from sources with a water potential higher than their own. For aquatic plants, the source is the surrounding aqueous medium. In freshwater environments, the presence of solutes in the plant's cells creates a water potential gradient from the surrounding water to the plant. In marine environments, plants must lower their water potential below that of seawater to take up water. Marine plants, as well as terrestrial plants of salt marshes and saline soils, adjust their osmotic potential in a manner similar to that of microorganisms by synthesizing solutes and taking up inorganic salts from their environment. Inorganic salts must be taken up selectively, however, because some (e.g., Na^+, Cl^-) can be toxic at high concentrations. The cell membranes of plants act as a solute filter, determining the amounts and types of solutes that move into and out of the plant.

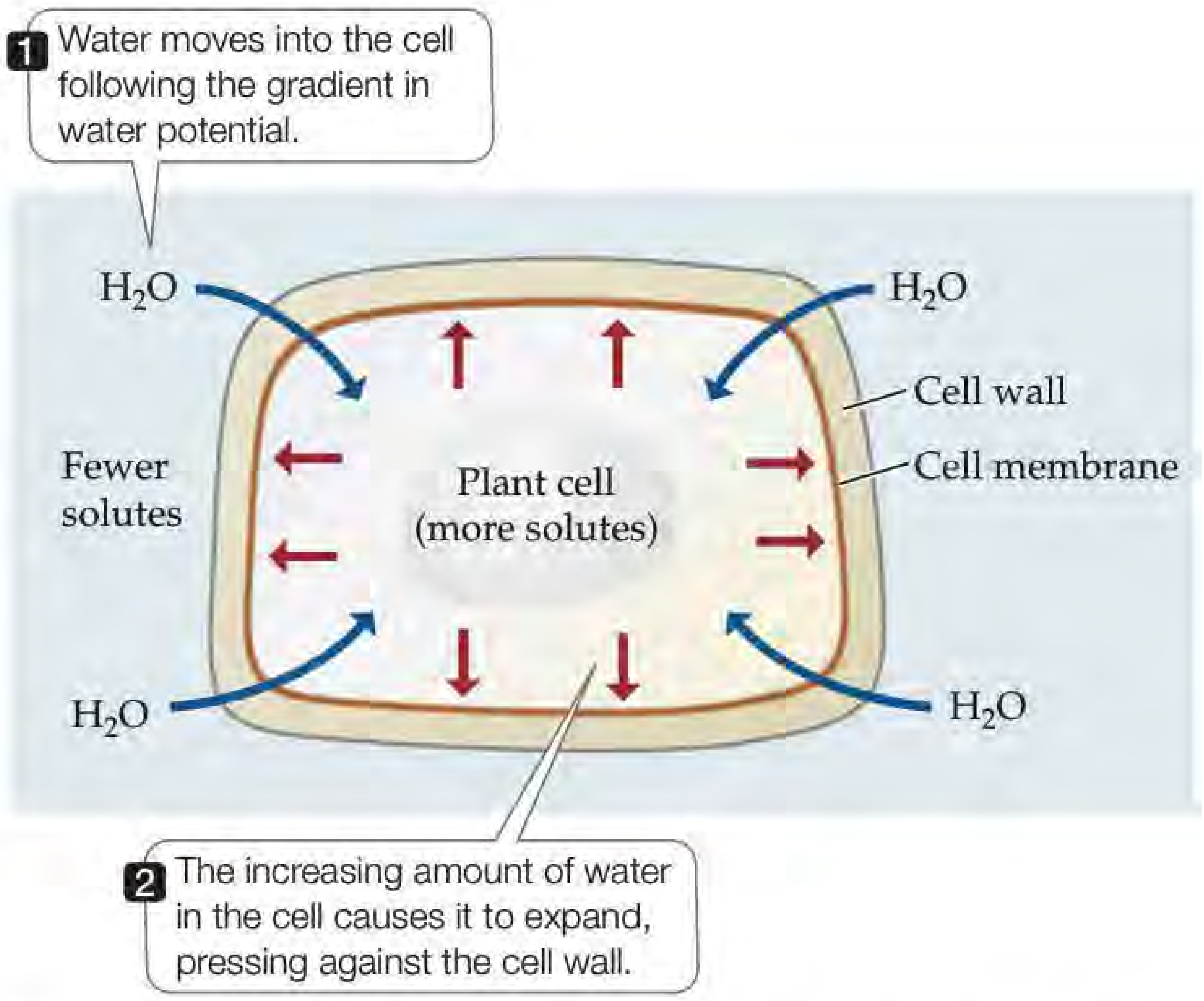


Figure 4.19 Turgor Pressure in Plant Cells When a plant cell is surrounded by water with a solute concentration lower than its own, water moves into the cell, while solutes in the cell are prevented from moving out by the cell membrane. The increasing amount of water in the cell causes the cell to expand, pressing against the cell wall.

Terrestrial plants acquire water from the soil through their roots, as well as through associations with mutualistic fungi that grow into their roots from the soil, called *mycorrhizae* (see Concept 15.1). The earliest land plants, which had not yet evolved roots, used mycorrhizal fungi to take up water and nutrients from the soil. The majority of modern terrestrial plant species use a combination of roots and mycorrhizae to take up water. Only the finest roots can take up water from the soil, because older, thicker roots develop a water-resistant waxy coating that limits their ability to absorb water as well as to lose water to the soil. Mycorrhizae provide a greater surface area for absorption of water and nutrients for the plant and allow greater exploration of the soil for these resources. In turn, the mycorrhizal fungi obtain energy from the plant.

Plants lose water by transpiration when their stomates open to allow CO_2 from the atmosphere to diffuse into their leaves. Water moves out through the stomates, following the water potential gradient from the inside of the leaf (100% relative humidity) to the air. As we saw in the previous section, transpiration is an important cooling mechanism for leaves. The plant must replace the water

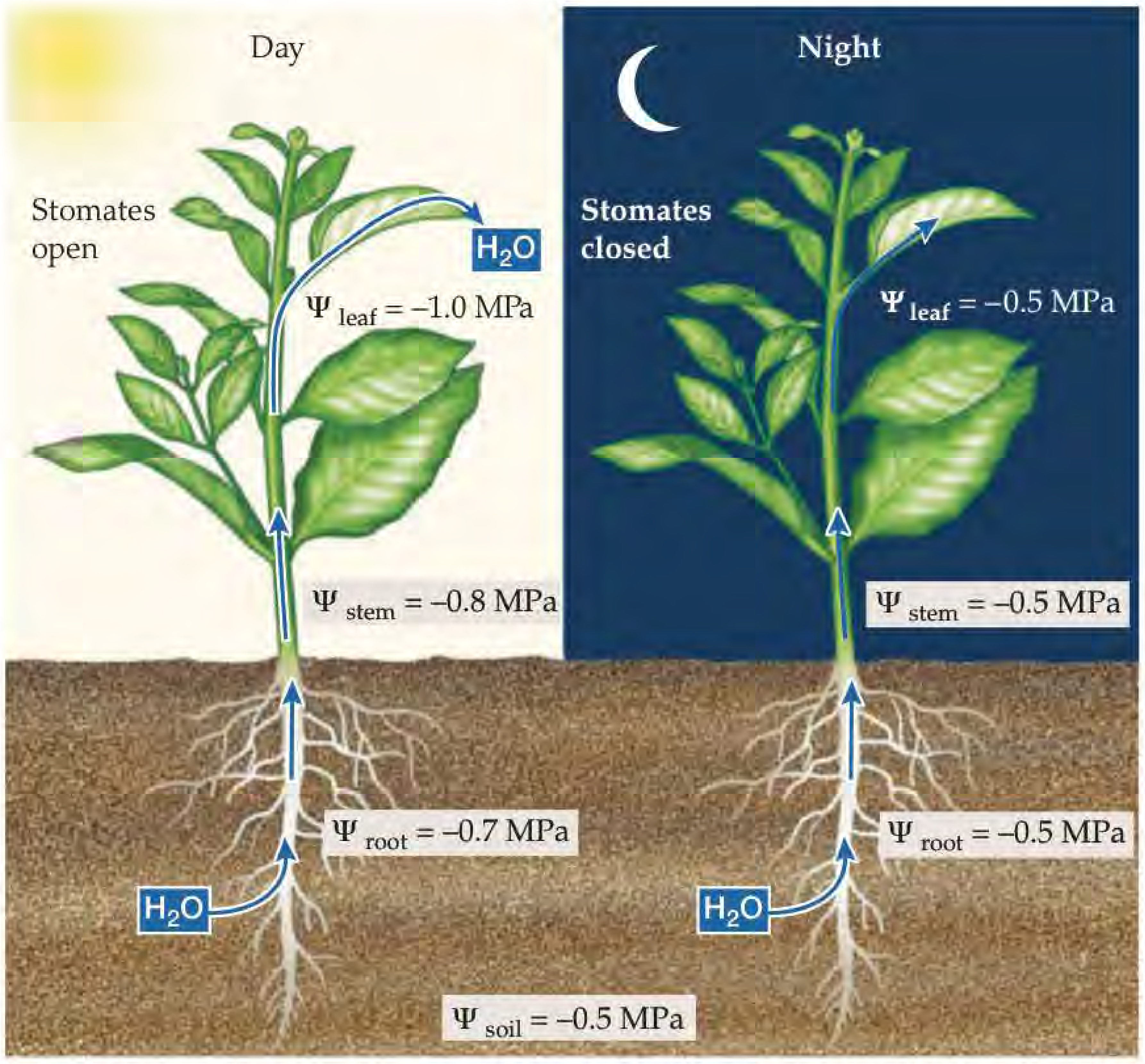


Figure 4.20 The Daily Cycle of Dehydration and Rehydration During the day, when the stomates are open, transpiration results in a gradient of water potential from leaf to stem, stem to roots, and roots to soil. At night, when the stomates are closed, water potential equilibrates as the plant rehydrates.

lost by transpiration, however, if it is to avoid water stress. As a leaf loses water, the water potential of its cells decreases, creating a water potential gradient between the leaf and the xylem in the stem to which it is attached, so water moves through the xylem into the leaf. In this way, when the plant is transpiring, it creates a gradient of decreasing water potential from the soil through the roots and stems to the leaves (**Figure 4.20**). Water therefore flows from the soil, which has the highest water potential, into the roots, the xylem, and eventually the leaves, from which it is lost to the atmosphere via transpiration. Because there is greater resistance to the movement of water into the roots and through the xylem than out through the stomates, the water supply from the soil cannot keep up with water loss by transpiration. As a result, the water content of the plant decreases during the day. At night the stomates close, and the water supply from the soil rehydrates the plant until it reaches near equilibrium with the soil water potential. This daily cycle of daytime dehydration and nighttime rehydration can go on indefinitely if the supply of water in the soil is adequate. The availability of water decreases when precipitation is not sufficient to replace the water lost from the soil through transpiration and evaporation. The water content of a plant will then decrease, and its turgor pressure will decrease as its cells become dehydrated (**Figure 4.21**). To avoid reaching a detrimentally or even lethally low water content, the plant must restrict its transpirational water loss. If leaf cells become so dehydrated that turgor is lost, the stomates close. This level of water stress can harm the plant, causing impairment of physiological functions such as photosynthesis. Extremely dry conditions can cause loss of xylem function (see **Web Extension 4.1**).

Some plants of seasonally dry environments shed their leaves during long dry periods to eliminate transpirational water loss. Others have a signaling system that helps prevent the onset of water stress. As the soil dries out, the roots send a hormonal signal (abscisic acid) to the guard cells, which close the stomates, lowering the rate of water loss. Plants of dry environments, such as deserts, grasslands, and Mediterranean-type ecosystems, generally have better control of stomatal opening than

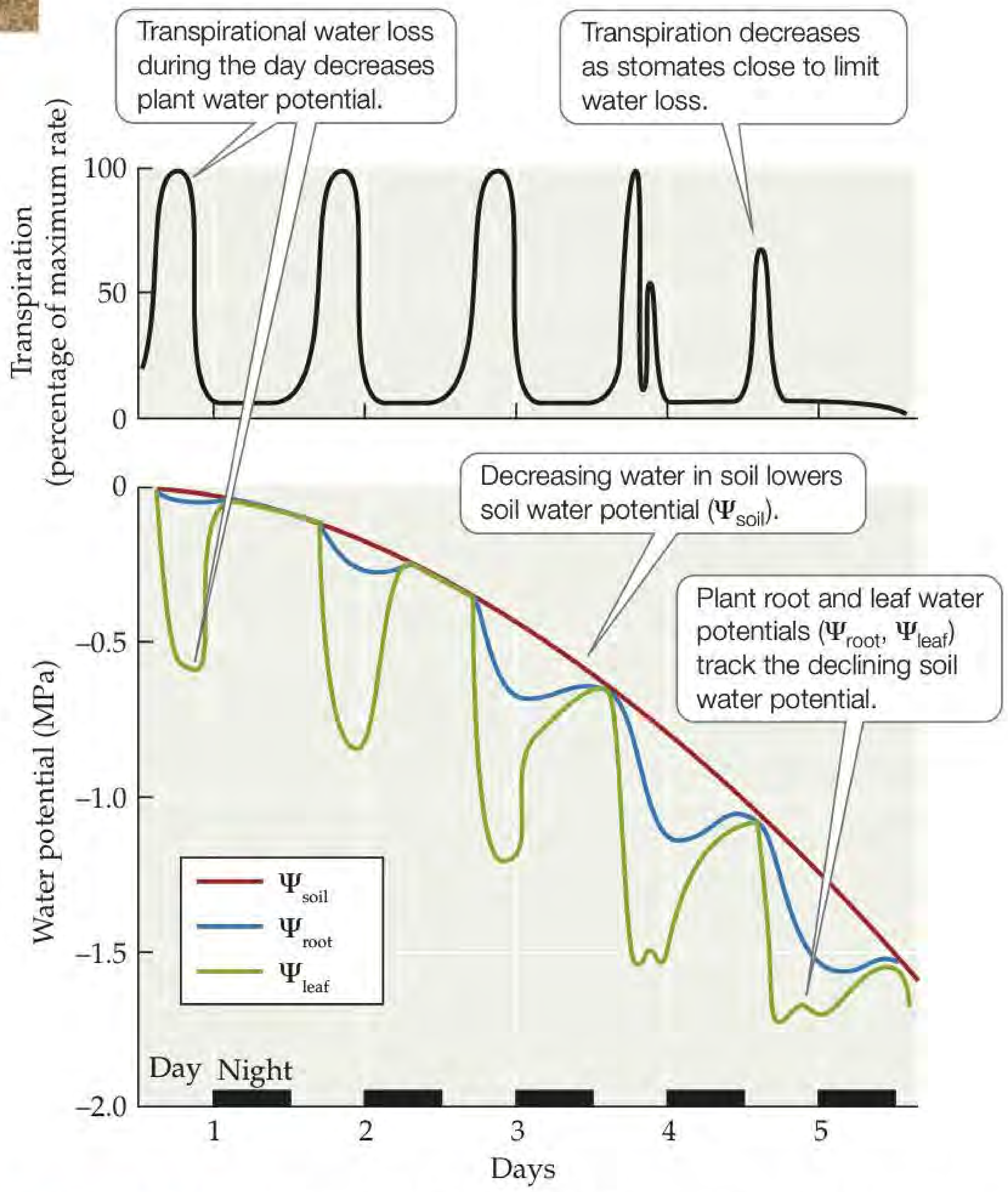


Figure 4.21 How Plants Cope with Depletion of Soil Water If soil water is not recharged, transpiration will deplete it, leading to progressive drying of the soil and a decrease in soil water potential.

? As the soil dries, stomates may close at midday and reopen later in the afternoon, as seen on day 4 in the graph. Assuming the air temperature is cooler later in the day, what influence would this have on plant water loss?

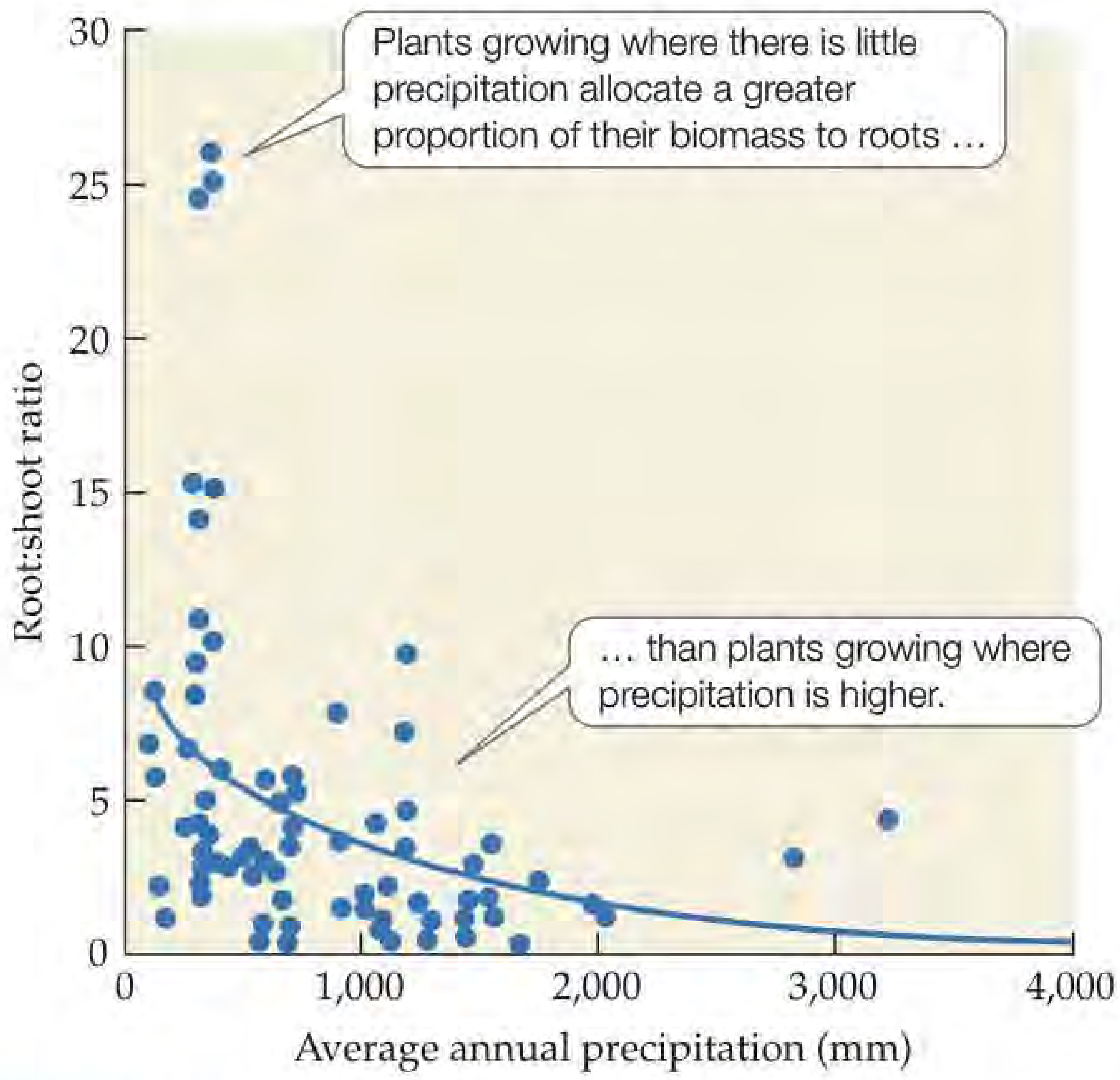


Figure 4.22 Allocation of Growth to Roots versus Shoots Is Associated with Precipitation Levels The ratio of root biomass to leaf and stem (shoot) biomass increases with decreasing precipitation in shrubland and grassland biomes. Allocation of more biomass to roots in dry soils provides more water uptake capacity to support leaf function. (After Mokany et al. 2006.)

plants of wetter climates. Plants of dry environments also have a thick waxy coating (cuticle) on their leaves to prevent water loss through the nonporous regions of the leaves. Additionally, plants of dry environments maintain a higher ratio of root biomass to biomass of stems and leaves than plants of moister environments, enhancing the rate of water supply to transpiring tissues (Mokany et al. 2006) (**Figure 4.22**). Some plants are capable of acclimatization by altering the growth of their roots to match the availability of soil moisture and nutrients.

Can plants have too much water? Technically, no, but saturation inhibits the diffusion of oxygen and can cause hypoxia in plant roots. Thus, waterlogged soils inhibit aerobic respiration in roots. Wet soils also enhance the growth of harmful fungal species that can damage roots. Ironically, the combination of these factors can lead to root death, which cuts off the supply of water to plants, and eventually to wilting. Adaptations to low oxygen concentrations in wet soils include root tissue containing air channels (called *aerenchyma*) as well as specialized roots that extend vertically above the water or waterlogged soil (as in mangroves; see Figure 3.19).

WATER BALANCE IN ANIMALS Multicellular animals face the same challenges plants and microorganisms do in maintaining water balance. Water losses and gains in animals, however, are governed by a more diverse set of exchanges than in plants and microorganisms (**Figure 4.23**). Many animals have the added complexity of specialized organs for gas exchange, ingestion and digestion, excretion, and circulation, all of which create areas of localized water and solute exchange as well as gradients of water and solutes within the animal's body. Most animals are mobile and can seek out environments conducive to maintaining a favorable water and solute balance, an option not available to plants or to most microorganisms.

Many animals must be able to maintain favorable water and solute balances under conditions of varying salinity. A marine animal that lacks this ability will die if transferred to brackish or fresh water. Although most marine invertebrates are isoosmotic to seawater, the specific types of solutes in their bodies can vary. Many invertebrates

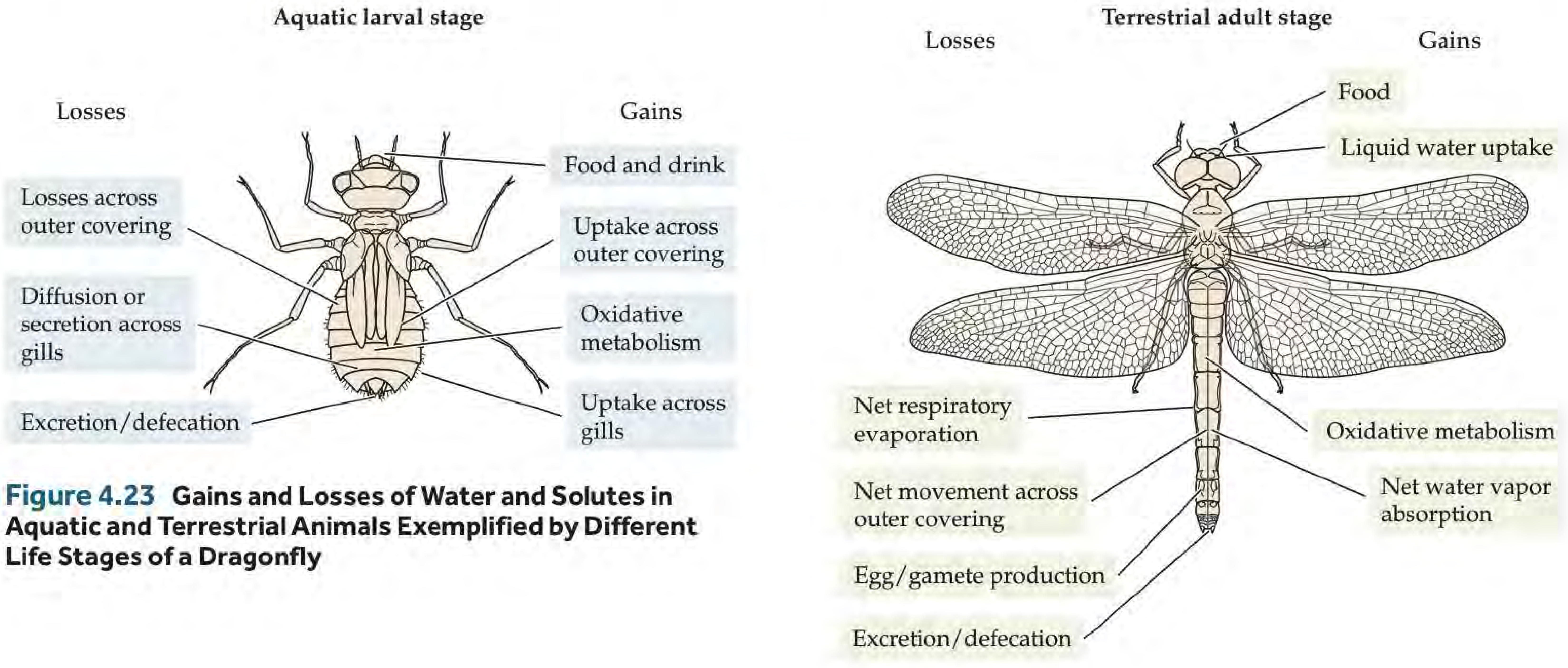


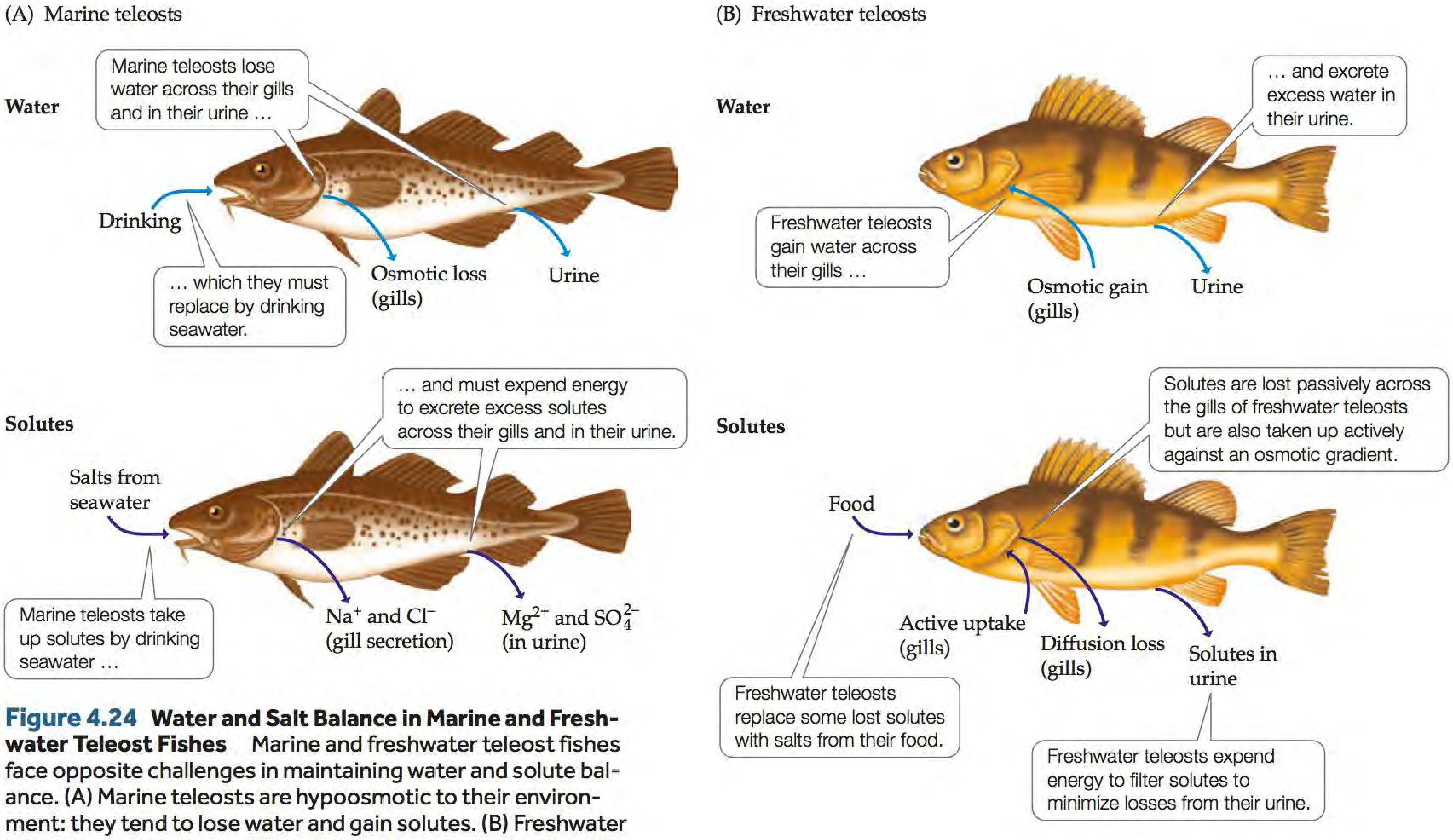
Figure 4.23 Gains and Losses of Water and Solutes in Aquatic and Terrestrial Animals Exemplified by Different Life Stages of a Dragonfly

that are capable of adjusting to changes in the solute concentration of their environment do so by exchanging solutes with the surrounding seawater. Like plants, these animals must selectively control this exchange of specific solutes because some external solutes are toxic at the concentrations at which they are found in seawater, and because some internal solutes are needed for biochemical reactions. Jellyfishes, squids, and crabs, for example, have sodium (Na^+) and chloride (Cl^-) concentrations similar to those of seawater, but their sulfate (SO_4^{2-}) concentrations may be one-half to one-fourth of those found in seawater.

Marine vertebrates include animals that are isoosmotic and hypoosmotic to seawater. The cartilaginous fishes, including the sharks and rays, have blood solute concentrations similar to those of seawater, although, as in invertebrates, their concentrations of specific solutes differ from those in seawater. In contrast, marine teleost (bony) fishes and mammals evolved in fresh water and later moved into marine environments. Their blood is hypoosmotic to seawater. Fish exchange water and salts with their environment through drinking and eating, and across the gills, which are also the organs of O_2 and CO_2 exchange (**Figure 4.24A**). Salts that diffuse into or are ingested by marine teleost fishes must be continuously excreted in urine and through the gills against an osmotic gradient, which requires an expenditure of energy. Water lost across the gills must be replaced by drinking. Marine mammals, such as whales and porpoises, produce urine that is hyperosmotic to seawater and avoid drinking seawater to minimize salt uptake.

Freshwater animals are hyperosmotic to their environment; therefore, they tend to gain water and lose salts. Most salt exchange occurs at the gas exchange surfaces, including the skin of some invertebrates (e.g., freshwater worms) and the gills of many vertebrates and invertebrates. These animals must compensate for salt losses by taking up solutes in their food, and some groups, such as teleost fishes, must take up solutes actively through the gills against an osmotic gradient (**Figure 4.24B**). Excess water is excreted as dilute urine, from which the excretory system actively removes solutes to minimize their loss.

Terrestrial animals face the challenge of exchanging gases (O_2 and CO_2) in a dry environment with a very low water potential. These animals lower their evaporative water loss and exposure to water stress by having skin with a high resistance to water loss or by living in environments where they can compensate for high water losses with high water intake. Both approaches involve


(A) Marine teleosts

(B) Freshwater teleosts

Marine teleosts lose water across their gills and in their urine …

… which they must replace by drinking seawater.

… and must expend energy to excrete excess solutes across their gills and in their urine.

Marine teleosts take up solutes by drinking seawater …

… and excrete excess water in their urine.

Freshwater teleosts gain water across their gills …

Solutes are lost passively across the gills of freshwater teleosts but are also taken up actively against an osmotic gradient.

Freshwater teleosts replace some lost solutes with salts from their food.

Freshwater teleosts expend energy to filter solutes to minimize losses from their urine.

Figure 4.24 Water and Salt Balance in Marine and Freshwater Teleost Fishes Marine and freshwater teleost fishes face opposite challenges in maintaining water and solute balance. (A) Marine teleosts are hypoosmotic to their environment: they tend to lose water and gain solutes. (B) Freshwater teleosts are hyperosmotic to their environment: they tend to gain water and lose solutes.

TABLE 4.1 Ranges of Tolerances for Water Loss in Selected Animal Groups

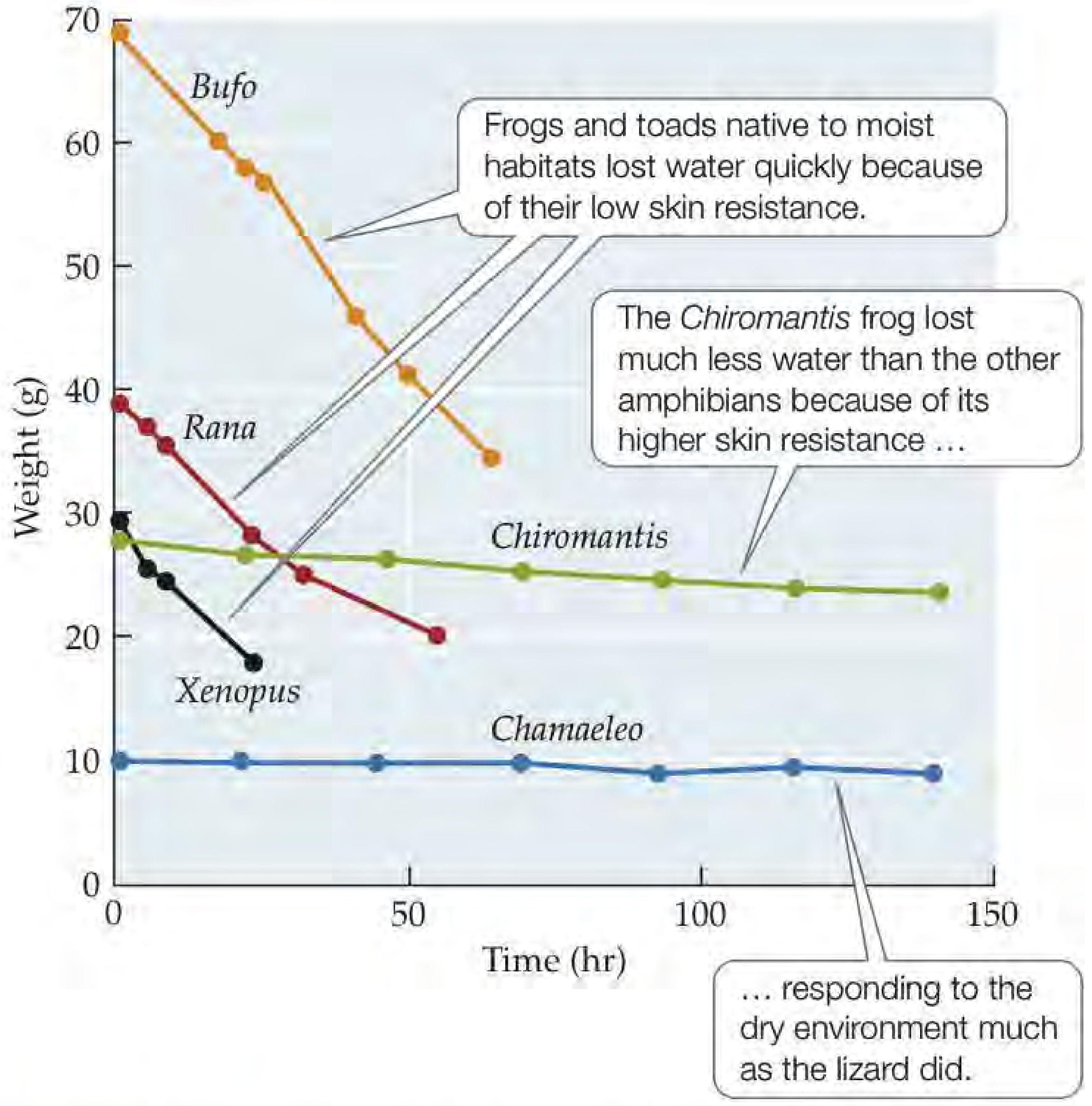
GROUP	WEIGHT LOSS (%)
Invertebrates	
Mollusks	35–80
Crabs	15–18
Insects	25–75
Vertebrates	
Frogs	28–48
Small birds	4–8
Rodents	12–15
Human	10–12
Camel	30

Source: Willmer et al. 2005.

Note: Values are maximum percentages of body weight lost as water that can be tolerated, based on observations of a range of exemplary species in each group.

risks and trade-offs, however. A high resistance to water loss may compromise the animal's ability to exchange gases with the atmosphere. Reliance on a steady water supply puts the animal at risk if the source of water fails (e.g., during a severe drought). Tolerance for water loss varies substantially among groups of terrestrial animals. Generally, invertebrates have a higher tolerance for water loss than vertebrates. Within the vertebrates, amphibians have a higher tolerance for, but lower resistance to, water loss than mammals and birds (**Table 4.1**).

Amphibians, including frogs, toads, and salamanders, rely primarily on stable water supplies to maintain their water balance. They can be found in a wide variety of biomes, from tropical rainforests to deserts, as long as there is a reliable source of water, such as regular rains or ponds. Amphibians depend on gas exchange through the skin to a greater degree than other terrestrial vertebrates. Therefore, amphibian skin is often thin, with a low resistance to water loss (**Figure 4.25**). However, some adult amphibian species have adapted to dry environments by developing specialized skin with higher resistance to water loss. For example, the southern foam-nest tree frog (*Chiromantis xerampelina*), which occurs throughout Africa, has skin that resists water loss in a manner similar to that of lizards. To compensate for reduced gas exchange through the skin, it has a higher breathing rate (Stinner and Shoemaker 1987). As a group, tree frogs have higher skin resistance to water loss than ground frogs, reflecting their drier habitat. Some ground frogs of seasonally dry environments, such as the northern snapping frog (*Cyclorana australis*) of Australia, lower their rates of water loss by forming a "cocoon" of mucous secretions consisting of proteins and fats that increases resistance to water loss.



Frogs and toads native to moist habitats lost water quickly because of their low skin resistance.

The *Chiromantis* frog lost much less water than the other amphibians because of its higher skin resistance …

… responding to the dry environment much as the lizard did.

Figure 4.25 Resistance to Water Loss Varies among Frogs and Toads Amphibians were kept under uniform dry environmental conditions (25°C, 20%–30% relative humidity) to examine their rates of water loss, measured as loss of body weight. A lizard (*Chamaeleo*) was also tested for comparative purposes.

? How could you estimate the resistances of these species to water loss quantitatively using this graph?

Reptiles have been extremely successful at inhabiting dry environments. The thick skin of desert snakes and lizards provides protection for the internal organs as well as an effective barrier to water loss. The outer skin, made up of multiple layers of dead cells with a fatty coating, is overlain by plates or scales. These layers give reptilian skin a very high resistance to water loss. Mammals and birds have skin anatomy similar to that of reptiles but have hair or feathers covering the skin rather than scales. The presence of sweat glands in mammals represents a trade-off between resistance to water loss and evaporative cooling. The highest resistances to water loss among terrestrial animals are found in the arthropods (e.g., insects and spiders), which are characterized by an outer exoskeleton made of hard chitin and coated with waxy hydrocarbons that prevents water movement (**Table 4.2**).

An instructive example of how animals use a variety of integrated adaptations to cope with arid environments involves kangaroo rats (*Dipodomys* spp.), found throughout the deserts of North America. A combination of efficient water use and low rates of water loss greatly diminishes these rodents' water requirements (Schmidt-Nielsen and Schmidt-Nielsen 1951) (**Figure 4.26**). Kangaroo rats rarely drink water. A large proportion of their water requirement is met by eating dry seeds and by oxidative metabolism—that is, by metabolically converting carbohydrates and fats into water and carbon dioxide (Schmidt-Nielsen 1964). The animals also consume water-rich foods, such as insects or succulent vegetation, if they are available.

Kangaroo rats minimize water loss through several physiological and behavioral adaptations. During the

TABLE 4.2 Ranges of Resistance of External Coverings (Skin, Cuticle) to Water Loss

GROUP	RESISTANCE (S/CM)
Crabs (marine)	6–14
Fish	2–35
Frogs	3–100
Earthworms	9
Birds	50–158
Desert tortoises	120
Desert lizards	1,400
Desert scorpions, spiders	1,300–4,000

Source: Willmer et al. 2005.

hottest periods of the year, they are active only at night, when air temperatures are lowest and humidities highest. During the day, they stay in their underground burrows, which are cooler and more humid than the desert surface. In some parts of their range, however, temperatures even in their burrows can rise high enough to expose kangaroo rats to significant evaporative water loss (Tracy and Walsberg 2002). To increase their resistance to this loss, kangaroo rats have thicker, oilier skin, with fewer sweat glands, than related rodents of moister environments. They minimize water losses in their urine and feces through effective removal of water by their kidneys and intestines. Kangaroo rats produce some of the most concentrated urine of any animal. The combination of these characteristics allows kangaroo rats to inhabit very arid environments without exposure to water stress, even without access to drinking water.

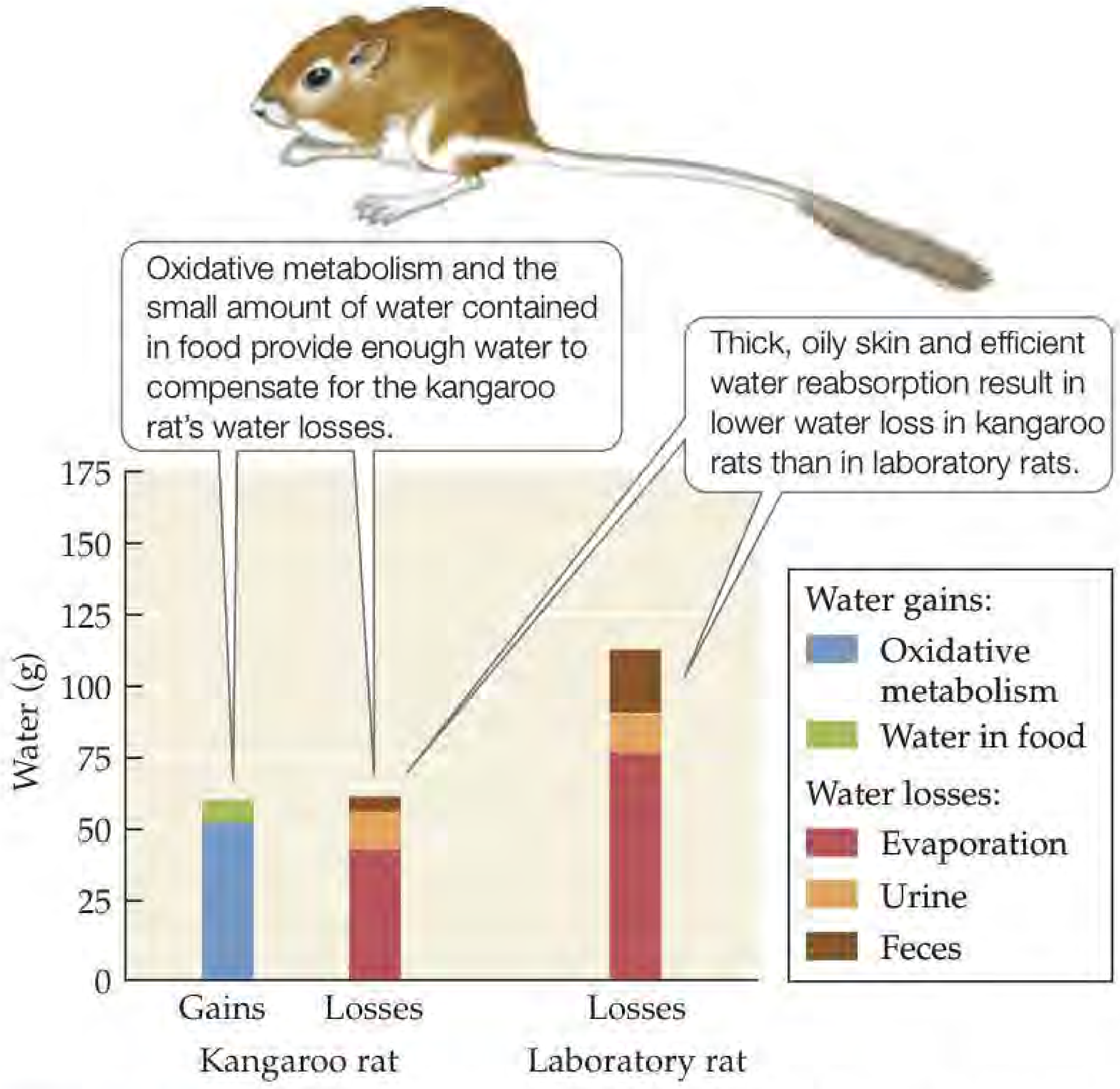


Figure 4.26 Water Balance in the Kangaroo Rat Under dry laboratory conditions (25°C, 25% relative humidity), kangaroo rats, native to deserts of western North America, do not require liquid water to survive. (After Schmidt-Nielson 1997.)

A CASE STUDY REVISITED

Frozen Frogs

The existence of amphibians above the Arctic Circle seems improbable, given their reliance on a steady supply of liquid water to maintain their water balance and the high potential for damage associated with freezing. Several problems must be overcome in order for complex organisms to survive freezing. First, when water freezes, it forms needle-like crystals that can penetrate and damage or destroy cell membranes and organelles. Second, the supply of oxygen to tissues is severely restricted by the lack of circulation and breathing. Finally, as ice forms, pure water is pulled from cells, resulting in shrinkage and an increase in solute concentration. Any one of these factors, or all of them working in combination, will kill tissues and organisms in subfreezing temperatures. Yet the frogs described in the Case Study, as well as many species of invertebrates, can tolerate the freezing of a substantial amount of their body water.

Wood frogs and other freeze-tolerant amphibians spend winter in shallow depressions under leaves, moss, or logs, which do not protect them from subfreezing temperatures. Several adaptations facilitate the survival of these amphibians through the winter and allow them to emerge from their frozen state in spring unharmed. Freezing of water in these animals is limited to the spaces outside the cells. A substantial proportion of their body water, from 35% to 65% in "fully frozen" frogs, freezes (Pinder et al. 1992). If more than 65% of their body water is frozen, most individuals will die because of excessive cell shrinkage. The formation of ice outside the cells is enhanced by the existence of ice-nucleating proteins that serve as the site of slow, controlled ice formation (Storey 1990). Solute concentrations in the unfrozen cells increase as the cells lose water to extracellular ice formation. In addition, freeze-tolerant amphibians synthesize additional solutes, including glucose and glycerol derived from the breakdown of liver glycogen. The resulting increase in solute concentrations lowers the freezing point inside the cells, allowing the intracellular solution to remain liquid at subfreezing temperatures. The concentrated solutes also stabilize the cell volume and the structures of organelles, proteins, and enzymes. As freezing proceeds, the frog's heart stops, and its lungs cease to pump air. Once it reaches this semi-stable state of partial freezing, the frog can remain frozen for several weeks, as long as the temperature does not drop below about –5°C (23°F). Although their winter "quarters" are not far below the surface of the ground, the insulating cover of leaves and snow keeps the frogs above that temperature.

The freezing process is initiated in wood frogs within minutes of ice formation within the animal, although the full process occurs over several days to weeks (Layne and Lee 1995). Thawing, on the other hand, may be rapid, with normal body functioning returning within 10 hours. (A video of the freezing and thawing of frogs can be seen at www.pbs.org/wgbh/nova/nature/frozen-frogs.html.) This amazing amphibian feat of spending winter in a semi-frozen state and emerging unharmed in spring has provided information to medical science that has facilitated the preservation of human tissues and organs at low temperatures (Costanzo et al. 1995), as well as optimism to proponents of whole-body cryonics, who hope that someday Grandpa can finally leave the Tuff Shed.

CONNECTIONS IN NATURE

Desiccation Tolerance, Body Size, and Rarity

As we saw in Chapter 3, there is a close association between organisms' adaptations to climate conditions and their distribution among terrestrial biomes. While subfreezing temperatures are an important constraint on the distribution and functioning of organisms in high-latitude and high-elevation biomes, low water availability is a more widespread challenge. Arid conditions can occur in most terrestrial biomes (see the climate diagrams in Concept 3.1), and they regularly occur over more than 60% of the land surface. As we have seen, the majority of terrestrial organisms, particularly animals, avoid exposure to dry conditions and rely on minimizing water losses to the environment. Some organisms, however, can tolerate arid conditions in much the same way that frozen frogs tolerate subfreezing winter conditions: by entering a dormant state while allowing themselves to dry out. This adaptive approach is common in microorganisms, including bacteria, fungi, and protists, but is also found in some multicellular animals and some plants, including mosses, liverworts, and a few flowering plants (Alpert 2006).

Desiccation-tolerant organisms can survive extreme dehydration, losing 80%–90% of their water as they equilibrate with the humidity of the air, then regain metabolic function shortly after they are rehydrated (**Figure 4.27**). As its cells dry out, the organism synthesizes sugars, which

(A) *Selaginella lepidophylla* (club moss)

(B) Tardigrade (water bear)

Figure 4.27 Desiccation-Tolerant Organisms (A) The leaves of the club moss *Selaginella lepidophylla* reach a very low moisture content during prolonged periods without rain (left); within 6 hours of receiving water, the leaves are functional and carrying out photosynthesis (right). (B) Water bears (tardigrades) are small invertebrates (less than 1 mm in length) found in aqueous environments, including oceans, lakes and ponds, soil water, and the water films on vegetation. Water bears contract and cease metabolism when they and their environment dry up (left) but rehydrate when moisture returns (right).

are the key to protecting its cell and organelle structures (Alpert 2006). Once dehydration proceeds beyond a certain threshold, metabolism ceases, and the sugars and the small amount of remaining water form a glassy coating over the cellular constituents. As with recovery from freezing, recovery from dehydration is rapid, occurring in hours to days.

The prevalence of dry conditions in terrestrial environments suggests that desiccation tolerance should be more common than it is. Why hasn't such tolerance evolved in more plants and animals? A clue to this puzzle may be the small size of the organisms that are desiccation-tolerant (Alpert 2006). Small organisms (less than 5 mm in animals) do not require structural reinforcements, such as a skeletal system, that would restrict the necessary shrinking of the organism as it dehydrates. In addition, water loss during dehydration must be slow enough to allow sugar synthesis to occur, but not so slow that the organism spends a long time with a low water content while metabolism is still occurring, which can cause physiological stress. Small organisms have surface area-to-volume ratios and thicknesses favorable for the water loss rates required.

These arguments explain why desiccation tolerance is more common in small organisms, but not why they are rare (see Chapter 23). The two characteristics—small size and rarity—are intimately linked. As we will see in Chapter 14, small size is often associated with slow growth rates and poor competitive ability under conditions of low resource availability. Thus, natural selection for desiccation tolerance may involve trade-offs with other ecological characteristics, such as competitive ability, that might prevent these organisms from being successful in competitive environments.

Summary

CONCEPT 4.1 Each species has a range of environmental tolerances that determines its potential geographic distribution.

- The physical environment affects an organism's ability to obtain energy and resources, thereby determining its growth and reproduction and, more immediately, its ability to survive the extremes of that environment. The physical environment is therefore the ultimate constraint on the geographic distribution of a species.
- Individual organisms can respond to environmental change through acclimatization, a short-term adjustment of the organism's physiology, morphology, or behavior that lessens the effect of the change and minimizes the associated stress.
- A population may respond to unique environmental conditions through natural selection for physiological, morphological, and behavioral traits, known as adaptations, that enhance individuals' survival, growth, and reproduction under those conditions.

CONCEPT 4.2 The temperature of an organism is determined by exchanges of energy with the external environment.

- Temperature controls physiological processes through its effects on enzymes and membranes.
- Gains of energy from and losses of energy to the external environment determine an organism's temperature. Modifying this exchange of energy with the environment allows an organism to control its temperature.
- Terrestrial plants may modify their energy balance by controlling transpiration, increasing or decreasing absorption of solar radiation, or adjusting the effectiveness of convective heat loss.
- Animals modify their energy balance mainly through behavior and morphology to adjust heat losses and gains and, in the case of endothermic animals, metabolic heat generation and insulation to lower heat loss.

CONCEPT 4.3 The water balance of an organism is determined by exchanges of water and solutes with the external environment.

- Water flows along energy gradients determined by solute concentration (osmotic potential), pressure or tension (pressure potential), and the attractive force of surfaces (matric potential).
- Plants and microorganisms can influence water potential by adjusting the solute concentration in their cells (osmotic adjustment).
- Aquatic animals that are hypoosmotic to the surrounding water must expend energy to excrete salts against an osmotic gradient. On the other hand, aquatic animals that are hyperosmotic to their environment must take up solutes from the environment to compensate for solute losses to the surrounding water.
- Terrestrial organisms can alter their gains or losses of water by adjusting their resistance to water movement, as by the opening or closing of stomates in plants or adaptations of the skin in animals.

Review Questions

1. Organisms exhibit different degrees of tolerance for environmental stresses. How does tolerance for variation in body temperature vary among plants, ectothermic animals, and endothermic animals? What factors influence the differences in tolerance among these groups? Can plants exhibit avoidance of temperature extremes?
2. Organismal adaptations to environmental conditions often affect multiple ecological functions, leading to associated trade-offs. The following are two different trade-offs to consider.
   a. Plants transpire water through their stomates. What effects does transpiration have on temperature regulation in leaves? What is the trade-off with transpirational temperature regulation in terms of leaf physiological function?
   b. Animals can more effectively warm their bodies by absorbing solar radiation if they are a dark color. Many animals, however, are not dark, but instead have a coloration close to that of their habitat (camouflage, as in the case of the basking lizard in Figure 4.15). What is the trade-off between animal coloration and heat exchange?
3. List several ways in which plants and animals in terrestrial environments influence their resistance to water loss to the atmosphere.

ON THE COMPANION WEBSITE
ecology4e.sinauer.com

The website includes companions to all of the Analyzing Data exercises, Online Quizzes, Flashcards, Suggested Readings, and more. In addition, the following resources are available for this chapter:

Hands-On Problem Solving

4.1 City Ants and Country Ants: Adaptation to Thermal Environments

Web Extensions

4.1 Cavitation and the Loss of Xylem Function

Online Climate Change Connection

4.1 Climate Change and Thermal Constraints on Foraging in Reptiles

Hone Your Problem-Solving Skills

Higher albedo leads to lower heat gain from solar radiation, and our earlier discussion of leaf pubescence in desert brittlebush (*Encelia*) species described the link between water availability, air temperature, and the amount of leaf pubescence. Where water is limiting for transpirational cooling and air temperatures are high, the native *Encelia* species have a higher amount of leaf pubescence relative to species from cooler, moister sites. Because there is a cost to building the leaf hairs, and a thick layer of hair potentially lowers photosynthesis rates, we might predict that in *E. farinosa*, which lives in the hot, dry desert, there is variation in the amount of leaf pubescence among populations in environments differing in water availability.

1. Populations of *E. farinosa* occur in Superior and Oatman, Arizona, and at Death Valley, California. Annual precipitation at the three sites is 453 mm, 111 mm, and 52 mm, respectively. What sites would you expect to have the most, least, and intermediate amounts of leaf pubescence? What site should exhibit the most seasonal change in leaf pubescence?
2. Using a graph of time (*x* axis) versus leaf absorption of solar radiation (*y* axis, using a relative scale from low to high), plot your predictions of the differences among the three populations as determined by variation in pubescence. Indicate any seasonal changes in pubescence you might expect as soils dry out.
3. The following data are from a controlled experiment run by Sandquist and Ehleringer (2003) to test whether there was ecotypic differentiation among the *E. farinosa* populations. Plants from each population were grown from seed in a common garden under a uniform environment for 2 months under well-watered conditions. The soils were then allowed to dry out for a month under warm temperatures. Leaf absorptance of solar radiation measurements (as percentage of the incoming light) were measured at three times: under well-watered conditions, halfway into the drydown, and under dry conditions after a month of no added water. Use the data to test the hypotheses you developed for Question 2 by plotting them on a graph with soil conditions on the *x* axis and absorptance on the *y* axis. Do the data support or refute your hypotheses about differences in pubescence among the populations and seasonal changes associated with decreased water availability and increased temperature?

SOIL CONDITION/ POPULATION	LEAF ABSORPTANCE (%)		
	SUPERIOR	OATMAN	DEATH VALLEY
Well-watered	74	70	66
Halfway	57	53	49
Dry	46	43	42

Coping with Environmental Variation: Energy

5

Toolmaking Crows: A Case Study

Humans employ a multitude of tools to enhance our ability to gather food to meet our energy needs. We use a highly mechanized system of planting, fertilizing, and harvesting crops to feed ourselves or the livestock that we consume. For thousands of years, we have used specialized tools to increase our efficiency of hunting prey, including spears, bows and arrows, and rifles. We view our toolmaking capacity as something that differentiates us from other animals.

However, we humans are not alone in using tools to enhance our food acquisition ability. In the 1920s, Wolfgang Köhler, a psychologist studying the behavior of chimpanzees, observed that chimps in captivity made tools to retrieve bananas stashed in areas that were difficult to reach (Köhler 1927). Jane Goodall, a prominent primatologist, reported observing chimpanzees in the wild using grass blades and plant stems to "fish" for termites in holes in the ground and in decaying wood (**Figure 5.1**). Although these reports challenged the commonly held belief that modern humans were the only makers of tools to enhance food acquisition, it was perhaps comforting to those clinging to this notion that the observations were associated with one of our closest extant relatives. No one would ever have suspected similar behavior in birds, touted as one of the least intelligent vertebrates, as evidenced by the dubious insult "birdbrain" exchanged between humans.

The corvids, a family of birds that includes crows, ravens, magpies, jays, and jackdaws, enter our cultural heritage with a reputation for being clever. Even so, the discovery that crows use food-collecting tools manufactured from plants was unexpected. Gavin Hunt reported in 1996 that the crows (*Corvus moneduloides*) of New Caledonia, an island in the South Pacific, used tools to snag insect larvae, spiders, and other arthropods and pull them from the wood of living and decomposing trees (Hunt 1996) (**Figure 5.2A**). Hunt found that individual birds used one of two types of tools, either (1) a hooked twig fashioned from a shoot stripped of its leaves and bark (**Figure 5.2B**) or (2) a serrated leaf clipped from a *Pandanus* tree (**Figure 5.2C**). Both tools were therefore manufactured, rather than just collected from materials lying on the ground.

Hunt described a unique foraging style used by the New Caledonian crows. The birds probed tree cavities or areas of

KEY CONCEPTS

CONCEPT 5.1 Organisms obtain energy from sunlight, from inorganic chemical compounds, or through the consumption of organic compounds.

CONCEPT 5.2 Radiant and chemical energy captured by autotrophs is converted into stored energy in carbon–carbon bonds.

CONCEPT 5.3 Environmental constraints have resulted in the evolution of biochemical pathways that improve the efficiency of photosynthesis.

CONCEPT 5.4 Heterotrophs have adaptations for acquiring and assimilating energy efficiently from a variety of organic sources.

Figure 5.1 Nonhuman Tool Use Chimpanzees use plant stems as tools to forage for termites. Chimpanzees were the first nonhuman animals documented using tools to forage for food.

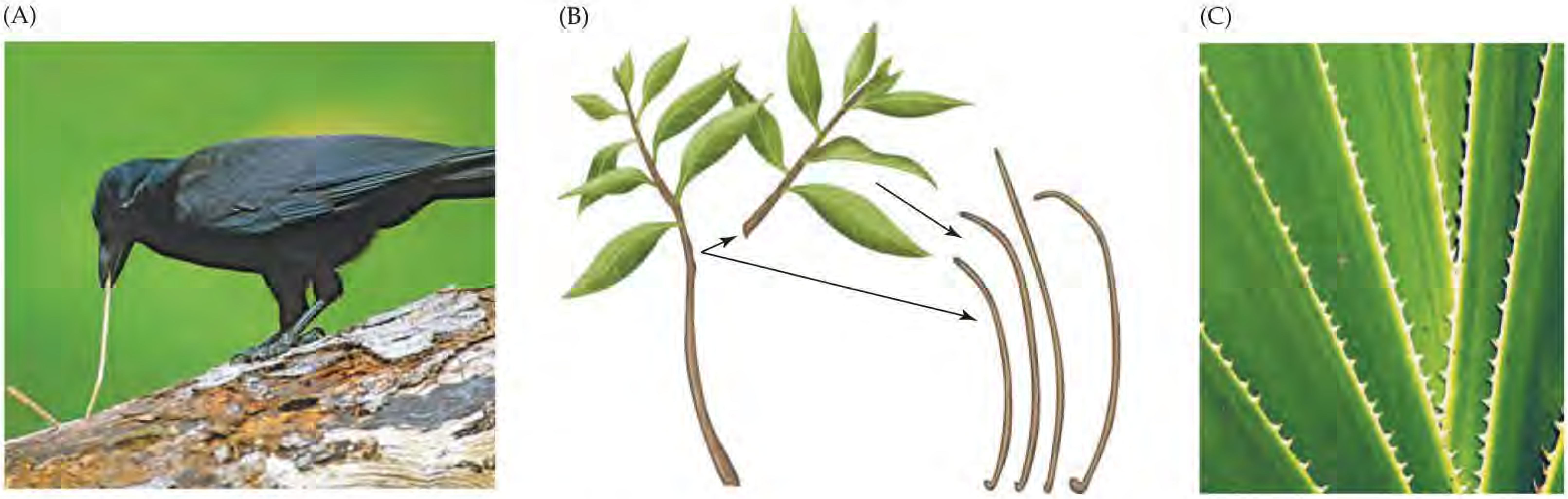


Figure 5.2 **Tools Manufactured by New Caledonian Crows** (A) Crows use the tools they make to probe for food in the cavities and crevices of trees. (B) Hooked twig tools, made from shoots of trees. The birds use their bills to form the hook while holding the stick with their feet. (C) The crows also can create tools from the serrated leaves of *Pandanus* plants. (B after Hunt 1996.)

dense foliage using their tools as extensions of their bills. The birds used the tools repeatedly, carrying them from tree to tree. The presence of hooks on both types of tools suggested an innovative element that might increase the birds' efficiency in extracting prey from their refuges in the trees. The tools also appeared to be uniform in their construction; Hunt examined 55 tools manufactured by different birds and found that they differed little. When New Caledonian crows were captured and brought into the laboratory, they made hooked tools from wire, and experiments showed that the tools increased their food retrieval efficiency (Weir et al. 2002).

Toolmaking at a skill level equivalent to that shown by the crows appeared in humans only in the late Stone Age, approximately 450,000 years ago (Mellars 1989). How have these birds achieved a similar level of sophistication in their tool construction? The high numbers of New Caledonian crows using tools, and the consistency in the construction of the tools, indicate a cultural phenomenon—a skill learned socially within a population of animals—that had never before been observed in birds. How much of an energetic benefit do the crows gain by using tools rather than just their bills?

Introduction

Energy is one of the most basic requirements for all organisms. Physiological maintenance, growth, and reproduction all depend on energy acquisition. Organisms are complex systems, and if energy input stops, so does biological functioning. Enzyme systems fail if replacement proteins are not made. Cell membranes degrade and organelles cease to operate without energy to maintain and repair them. In this chapter, we will review the different ways in which organisms acquire energy to meet the demands of cellular maintenance, growth, reproduction, and survival. We'll focus on the major mechanisms that allow organisms to obtain energy from their environment, including the capture of sunlight and chemical energy and the acquisition and use of organic compounds synthesized by other organisms.

CONCEPT 5.1
Organisms obtain energy from sunlight, from inorganic chemical compounds, or through the consumption of organic compounds.

Sources of Energy

We sense energy in our environment in a variety of forms. Light from the sun, a form of *radiant energy*, illuminates our world and warms our bodies. Objects that are cold or warm to our touch have different amounts of *kinetic energy*, which is associated with the motion of the molecules that make up the objects. A grasshopper eating a leaf and a coyote eating a meadow vole both represent the transfer of *chemical energy*, which is stored in the food that is being consumed. Radiant and chemical energy are the forms organisms use to meet the demands of growth and maintenance, while kinetic energy, through its influence on the rate of chemical reactions and temperature, is important for controlling the rate of activity and metabolic energy demand of organisms. A cold endotherm needs to warm its body to the optimal temperature for physiological functioning. It does this by "burning" chemical energy from its food during cellular respiration. Ultimately, this food was derived from the radiant energy of sunlight, converted into chemical energy by plants. Most of the energy used to support industrial development, fuel our cars, and heat our homes originated ultimately with photosynthesis, which produced the organisms that became the oil we pump out of the ground.

Autotrophs are organisms that assimilate energy from sunlight (*photosynthetic* organisms) or from inorganic chemical compounds in their environment (*chemosynthetic* archaea and bacteria).[1] Autotrophs convert the energy of sunlight or inorganic compounds into chemical energy stored in the carbon–carbon bonds of organic compounds, typically carbohydrates. **Heterotrophs** are organisms that obtain their energy by consuming energy-rich organic compounds made by other organisms—all of which ultimately originated with organic compounds synthesized by autotrophs. Heterotrophs include organisms that consume nonliving organic matter (*detritivores*); they include earthworms and fungi in soil that feed on detritus derived mainly from dead plants, as well as bacteria in lakes that consume dissolved organic compounds. Heterotrophs also include organisms that consume living organisms but do not necessarily kill them (*parasites* and *herbivores*), as well as consumers (*predators*) that capture and kill their food source (*prey*).

On the surface, the distinction between autotrophs and heterotrophs would seem to be clear-cut: all plants are autotrophs, all animals and fungi are heterotrophs, and archaea and bacteria include both autotrophs and heterotrophs. Things are not always so simple, however. Some plants have lost their photosynthetic function and obtain their energy by parasitism. Such plants, known as *holoparasites* (*holo*, "entire, whole"), have no photosynthetic pigments and are heterotrophs. Dodder (genus *Cuscuta*, with approximately 150 different species), for example, is a common plant parasite found throughout the world (**Figure 5.3A,B**) and is considered a major pest of agricultural species. Dodder attaches to its host plant by growing in spirals around the stem and penetrates the phloem of the host, using modified roots called haustoria, to take up carbohydrates. Other plants, known as *hemiparasites*, are photosynthetic but obtain some of their energy, as well as nutrients and water, from host plants (**Figure 5.3C**).

Conversely, animals can act as autotrophs, although this phenomenon is relatively rare. Their photosynthetic capacity is acquired by consuming photosynthetic organisms or by living with them in a close relationship known as a *symbiosis* (see Concept 15.1). Some sea slugs, for

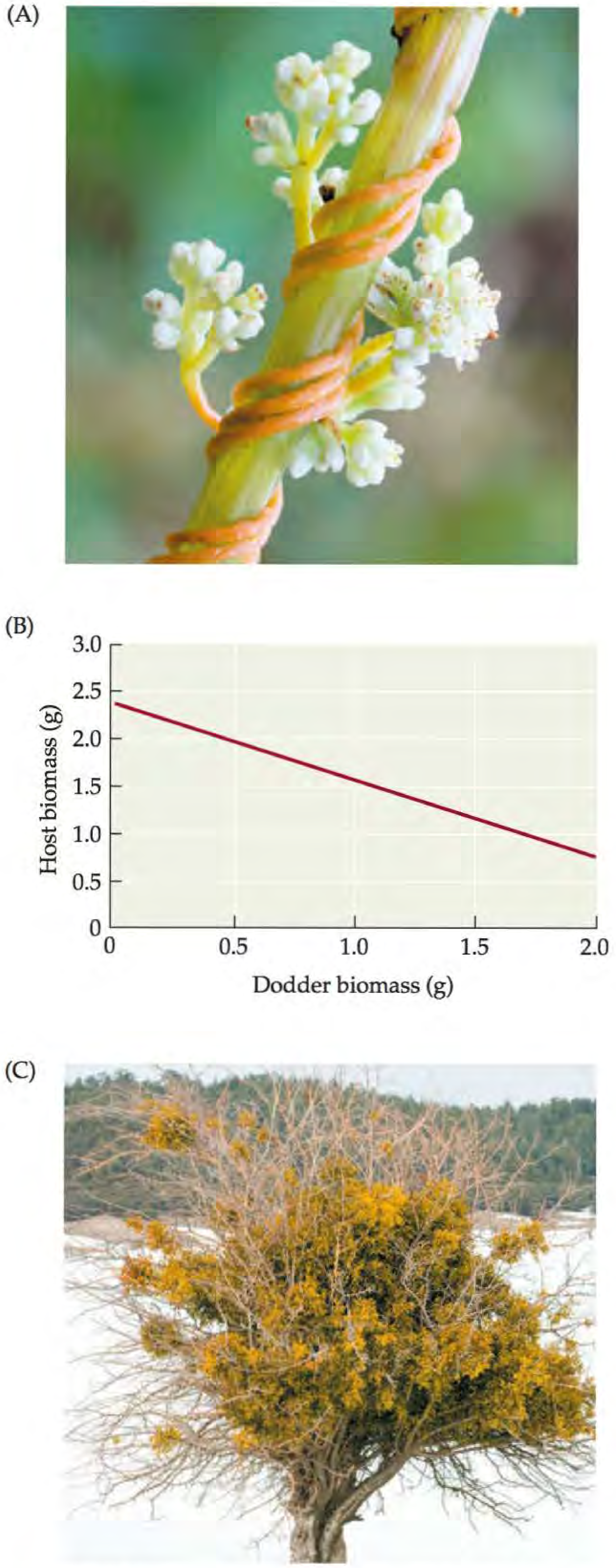


Figure 5.3 Plant Parasites (A) Dodder (*Cuscuta* sp.), a holoparasite that lacks chlorophyll, is shown here wrapped around the stem of a jewelweed plant. (B) Increasing amounts of European dodder (*Cuscuta europaea*) biomass result in decreasing growth of its host plant, stinging nettle (*Urtica dioica*). (C) Mistletoe is a hemiparasite: despite having photosynthetic tissues of its own, mistletoe draws water, nutrients, and some of its energy from its host tree. The red-berry mistletoe (*Viscum cruciatum*) seen here is often harvested and used as a holiday decoration. (B after Koskela et al. 2002.)

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[1] *Organic* chemical compounds have carbon–hydrogen bonds and are usually biologically synthesized. All other compounds are considered *inorganic* compounds.

Figure 5.4 Green Sea Slug The green color of this lettuce sea slug (*Elysia crispata*) is associated with the chloroplasts it has taken into its digestive system. The chloroplasts can supply enough energy to the sea slug to maintain it for several months without food.

example, have fully functional chloroplasts that supply them with carbohydrates through photosynthesis. These animals, in the order Ascoglossa, take intact chloroplasts from the algae they feed on into their digestive cells (**Figure 5.4**). The chloroplasts are maintained intact for up to several months, providing energy as well as camouflage to the sea slug.

In the next two sections, we'll take a more detailed look at the mechanisms autotrophs use to capture energy and at some of the adaptations that make that process more efficient. We'll do the same more generally for heterotrophs in the final section of this chapter. Chapters 12 and 13 will provide more detailed considerations of energy capture by heterotrophs, and Chapter 16 will look at the energetic relationships among the species in a community.

CONCEPT 5.2

Radiant and chemical energy captured by autotrophs is converted into stored energy in carbon–carbon bonds.

Autotrophy

The vast majority of the autotrophic production of chemical energy on Earth occurs through **photosynthesis**, a process that uses sunlight to provide the energy needed to take up carbon dioxide and synthesize organic compounds, principally carbohydrates. Although its contribution to the global energy picture is smaller, **chemosynthesis** (also known as *chemolithotrophy*), a process that uses energy from inorganic compounds to produce carbohydrates, is important to some key bacteria involved in nutrient cycling (see Concept 22.2) and in some unique ecosystems, such as hydrothermal vent communities (see the Case Study in Chapter 20). Because the energy derived from photosynthesis and chemosynthesis is stored in the carbon–carbon bonds of the organic compounds produced by these processes, ecologists often use carbon as a measure of energy.

TABLE 5.1 Inorganic Substrates Used by Chemosynthetic Bacteria as Electron Donors for Carbon Fixation

SUBSTRATE (CHEMICAL FORMULA)	TYPE OF BACTERIA
Ammonium (NH_4^+)	Nitrifying bacteria
Nitrite (NO_2^-)	Nitrifying bacteria
Hydrogen sulfide (H_2S/HS^-)	Sulfur bacteria (purple and green)
Sulfur (S)	Sulfur bacteria (purple and green)
Ferrous iron (Fe^{2+})	Iron bacteria
Hydrogen (H_2)	Hydrogen bacteria
Phosphite (HPO_3^{2-})	Phosphite bacteria

Source: Madigan and Martinko 2005.

Chemosynthesis harvests energy from inorganic compounds

The earliest autotrophs on Earth were probably chemosynthetic bacteria or archaea that evolved when the composition of the atmosphere was markedly different than it is today: low in oxygen, but rich in hydrogen, with significant amounts of carbon dioxide (CO_2) and methane (CH_4). A diverse group of archaea and bacteria still use energy from inorganic compounds to take up CO_2 and synthesize carbohydrates. Chemosynthetic bacteria are often named according to the inorganic substrate they use for energy (**Table 5.1**).

During chemosynthesis, organisms obtain electrons from the inorganic compound, or in other words, they *oxidize*[2] the inorganic substrate. They use the electrons to synthesize two high-energy compounds: adenosine triphosphate (ATP) and nicotinamide adenine dinucleotide phosphate (NADPH). They then use energy from ATP

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[2] Oxidation–reduction reactions involve the exchange of electrons between chemical compounds. The compound that gives up, or donates, electrons is oxidized, while the compound that accepts electrons is reduced.


Sulfur bacteria generate energy from hydrogen sulfide, leaving behind a residue of elemental sulfur.

Figure 5.5 Sulfur Deposits from Chemosynthetic Bacteria Sulfur bacteria thrive in sulfur hot springs with water temperatures as high as 110°C (230°F).

and NADPH to take up carbon from gaseous CO_2 (a process known as **fixation** of CO_2). The fixed carbon is used to synthesize carbohydrates or other organic molecules, which are stored to meet later demands for energy or biosynthesis (manufacture of chemical compounds, membranes, organelles, and tissues). Alternatively, some bacteria can use electrons from the inorganic substrate directly to fix carbon. The biochemical pathway most commonly used to fix carbon is the **Calvin cycle**, named for Melvin Calvin, the biochemist who first described it. The Calvin cycle is catalyzed by several enzymes, and it occurs in both chemosynthetic and photosynthetic organisms.

One of the most widespread and ecologically important groups of chemosynthetic organisms is the nitrifying bacteria (e.g., *Nitrosomonas*, *Nitrobacter*), which are found in both aquatic and terrestrial ecosystems. In a two-step process, these bacteria convert ammonium (NH_4^+) into nitrite (NO_2^-), then oxidize it to nitrate (NO_3^-). These chemical conversions of nitrogen compounds are an important component of nitrogen cycling and plant nutrition, and we will discuss them in more detail in Concept 22.2. Another important chemosynthetic group is the sulfur bacteria, associated with volcanic deposits, sulfur hot springs, and acidic mine wastes. Sulfur bacteria initially use the higher-energy forms of sulfur, H_2S and HS^- (hydrogen sulfide), producing elemental sulfur (S), which is insoluble and highly visible in the environment (**Figure 5.5**). Once the H_2S and HS^- are exhausted, these bacteria use elemental S as an electron donor, producing SO_4^{2-} (sulfate).

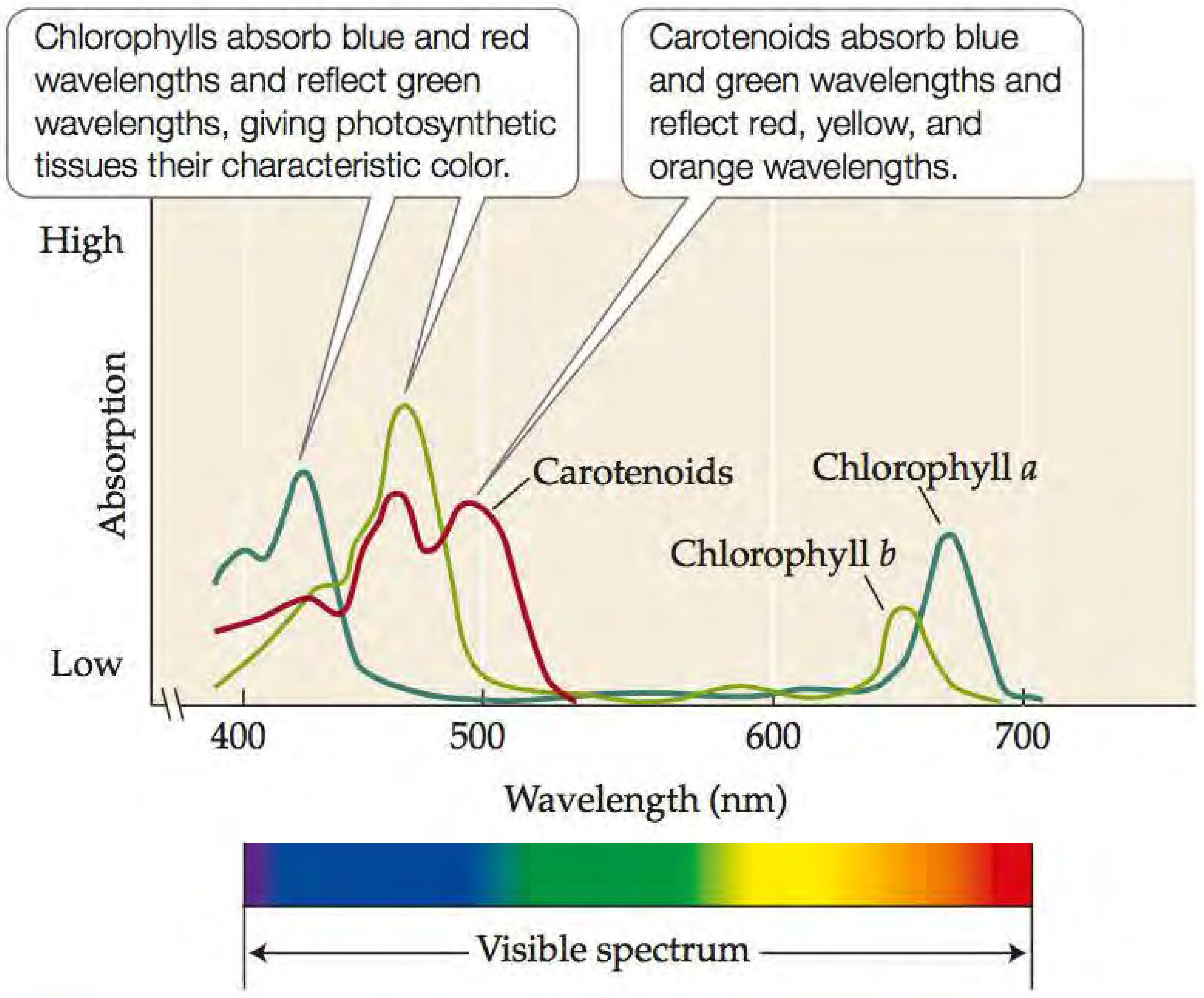
Photosynthesis is the powerhouse for life on Earth

Prior to 1650, most people believed that plants obtained the raw material needed for their growth from the soil. Jan Baptist van Helmont (1579–1644), a Flemish scientist, tested this theory experimentally. He carefully measured the mass of dry soil in a pot (200 pounds or 91 kg) and then planted a willow sapling weighing 5 pounds (2.3 kg). Van Helmont watered the sapling using only rainwater for 5 years as it grew into a small tree. At the end of that time, the tree had gained 164 pounds (74 kg), and the soil had lost only 2 ounces (0.06 kg). Although he incorrectly concluded that the tree had gained its mass from the water, van Helmont's experiment established the basis for the later discovery that photosynthetic uptake of CO_2 from the air—not material from the soil—was the source of the tree's weight gain.

The vast majority of biologically available energy on Earth is derived from the conversion of sunlight into energy-rich carbon compounds by photosynthesis. Photosynthetic organisms include some archaea, bacteria, and protists and most algae and plants. Leaves are the principal photosynthetic tissue in plants, but photosynthesis may also occur in stem and reproductive tissues. Like chemosynthesis, photosynthesis involves the conversion of CO_2 into carbohydrates that are used for energy storage and biosynthesis. Photosynthesis is also responsible for the largest movements of CO_2 between Earth and the atmosphere, and it is therefore critically important to the global climate system (as we'll see in Concept 25.1). Here, we will briefly review the major steps of plant photosynthesis and consider some ecologically relevant constraints on photosynthetic rates. In Concept 5.3, we will examine some variations in plant photosynthetic pathways.

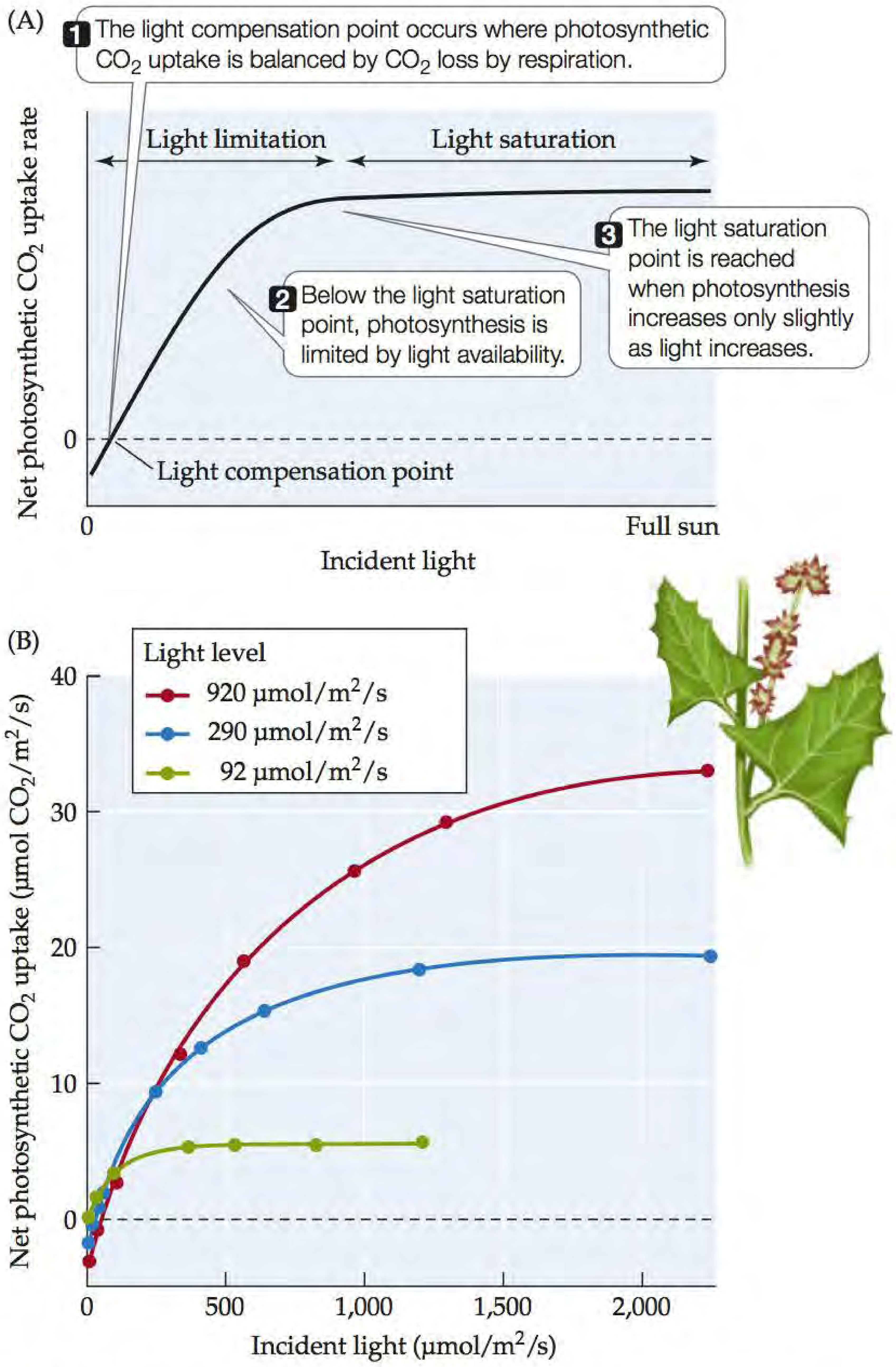
LIGHT-DRIVEN AND CARBON REACTIONS Photosynthesis has two major steps. The first is the harvesting of energy from sunlight, which is used to split water to provide electrons for generating ATP and NADPH. This step is often referred to as the *light-driven reactions* of photosynthesis. The second step is the fixation of carbon and the synthesis of sugars and subsequently carbohydrates. This step is often referred to as the *carbon reactions* of photosynthesis.

Sunlight harvesting is accomplished by several pigments, principally chlorophyll. Chlorophyll gives photosynthetic organisms their green appearance because it absorbs red and blue light and reflects green wavelengths (**Figure 5.6**). Plants and photosynthetic bacteria have similar chlorophyll pigments, but they absorb light at slightly different wavelengths. Additional pigments associated


Chlorophylls absorb blue and red wavelengths and reflect green wavelengths, giving photosynthetic tissues their characteristic color.

Carotenoids absorb blue and green wavelengths and reflect red, yellow, and orange wavelengths.

Figure 5.6 Absorption Spectra of Plant Photosynthetic Pigments Plants typically contain several light-absorbing pigments, which absorb light of different wavelengths.


1 The light compensation point occurs where photosynthetic CO_2 uptake is balanced by CO_2 loss by respiration.

2 Below the light saturation point, photosynthesis is limited by light availability.

3 The light saturation point is reached when photosynthesis increases only slightly as light increases.

Figure 5.7 Plant Responses to Variations in Light Levels (A) Photosynthetic light response curve. (B) Spearscale (*Atriplex triangularis*) plants grown at different light levels in growth chambers acclimatized to those light levels. Their light response curves indicate that adjustments in the light saturation point occurred. Small, but ecologically significant, changes in the light compensation point occur in many other species, facilitating CO_2 uptake at low light levels. (B after Björkman 1981.)

? Why might the light saturation point of a plant be below the maximum light level the plant is likely to be exposed to?

with photosynthesis, called accessory pigments, include the carotenoids, which are characteristically red, yellow, or orange in appearance. All of these photosynthetic pigments are embedded in a membrane, along with other molecules involved in the light-driven reactions. In plants, this membrane lies within specialized organelles called chloroplasts, while in photosynthetic bacteria the pigments are embedded in the cell membrane. The pigment molecules are arrayed like antennae, with each array containing between 50 and 300 molecules. The pigments absorb energy from discrete units of light, called *photons*. That energy is used to split water and provide electrons. The electrons are passed on to molecular complexes on the membranes, where they are used to synthesize ATP and NADPH.

The splitting of water (H_2O) to provide electrons for the light-driven reactions generates oxygen (O_2). The evolution of photosynthesis, and the accompanying release of O_2 into the atmosphere, was a critical step in the development of the chemistry of the modern atmosphere and lithosphere as well as the evolution of life on Earth. Atmospheric oxygen led to the creation of a layer of ozone (O_3) high in the atmosphere that shields organisms from high-energy ultraviolet radiation (described in Concept 25.4). The evolution of aerobic respiration, in which O_2 is used as an electron acceptor, facilitated great evolutionary changes for life on Earth.

In the carbon reactions of photosynthesis, energy from ATP and NADPH is used in the Calvin cycle to fix carbon. Carbon dioxide is taken up from the atmosphere through the stomates of vascular plants, or it diffuses across the cell membranes in nonvascular plants, algae, and photosynthetic bacteria and archaea. A key enzyme associated with the Calvin cycle is ribulose 1,5 bisphosphate carboxylase/oxygenase, thankfully usually referred to by its abbreviation, *rubisco*. Rubisco, the most abundant enzyme on Earth, catalyzes the uptake of CO_2 and the synthesis of a three-carbon compound: phosphoglyceraldehyde, or

PGA. PGA is eventually converted into a six-carbon sugar [glucose ($C_6H_{12}O_6$) in most plants]. The net reaction of photosynthesis is therefore

$$6\,CO_2 + 6\,H_2O \rightarrow C_6H_{12}O_6 + 6\,O_2 \qquad \textbf{(5.1)}$$

ENVIRONMENTAL CONSTRAINTS AND SOLUTIONS The rate of photosynthesis determines the supply of energy and substrates for biosynthesis available in the environment. Because this rate influences the growth and reproduction of photosynthetic organisms—often equated with their ecological success (their abundance and geographic range)—environmental controls on the rate of photosynthesis are a key topic in physiological ecology. It should be noted, however, that net energy (carbon) gain is also influenced by CO_2 losses associated with cellular respiration.

Light is clearly an important influence on rates of photosynthesis in both terrestrial and aquatic habitats. The relationship between the light level and a plant's photosynthetic rate can be portrayed by a *light response curve* (**Figure 5.7A**). When there is enough light that the plant's photosynthetic CO_2 uptake is balanced by its CO_2 loss by respiration, the plant is said to have reached the *light compensation point*. As the light level increases above the light compensation point, the photosynthetic rate also increases; in other words, photosynthesis is *limited* by the availability of light. The photosynthetic rate levels off at a *light saturation point*, which is typically reached at a level below full sunlight.

How do plants cope with light variation? How would an understory forest plant, for example, respond to shading by canopy trees? Could that plant acclimatize to more light if the canopy tree fell, allowing full sunlight to reach the ground? In a series of classic studies using controlled growth conditions, Olle Bjorkman demonstrated that acclimatization to different light levels involves a shift in the light saturation point (Bjorkman 1981) (**Figure 5.7B**). Morphological changes associated with this acclimatization include alterations in the thickness of leaves and variation in the number of chloroplasts available to harvest light (**Figure 5.8**). Photosynthetic organisms may also alter the density of their light-harvesting pigments—a strategy analogous to changing the size of the antenna on a radio—and the amounts of photosynthetic enzymes available for the carbon reactions. Typically, the average light level a plant experiences, integrated over the course of the day, is near the transition point between light limitation and light saturation (see **Analyzing Data 5.1**).

Some specialized bacteria are especially well adapted to photosynthesis at low light levels, which allows them to thrive in dimly lit environments such as relatively deep ocean water (down to about 20 m). A previously undescribed form of chlorophyll, called chlorophyll *f*, was recently found in samples of the marine cyanobacteria that form sediments in the shallow waters of Shark Bay, Australia (Chen et al. 2010), and has subsequently been found in cyanobacteria of other low-light habitats, including hot springs, rice paddies, and caves. Chlorophyll *f* absorbs light in the near-infrared region, just beyond the red wavelengths used by other forms of chlorophyll (see Figure 5.6). Chlorophyll *f* may be an adaptation that allows cyanobacteria possessing it to grow underneath other photosynthetic organisms that use light in the blue and red wavelengths, as it lets them harvest energy at wavelengths that pass through those other photosynthetic organisms. The discovery of a pigment that can harvest near-infrared energy has implications for increasing the efficiency of photovoltaic panels used to generate electricity, which may help lower emissions of CO_2 (see **Online Climate Change Connection 5.1**).

Water availability is an important control on the supply of CO_2 for photosynthesis in terrestrial plants. As we saw in Concept 4.3, low water availability results in closure of the stomates, restricting the entry of CO_2 into leaves. Stomatal control represents an important tradeoff for the plant: water conservation versus energy gain through photosynthesis as well as cooling of the leaf through transpiration. Keeping stomates open while tissues lose water can permanently impair physiological processes in the leaf. Closing stomates, however, not only limits photosynthetic CO_2 uptake, but also increases the chances of light damage to the leaf. When the Calvin

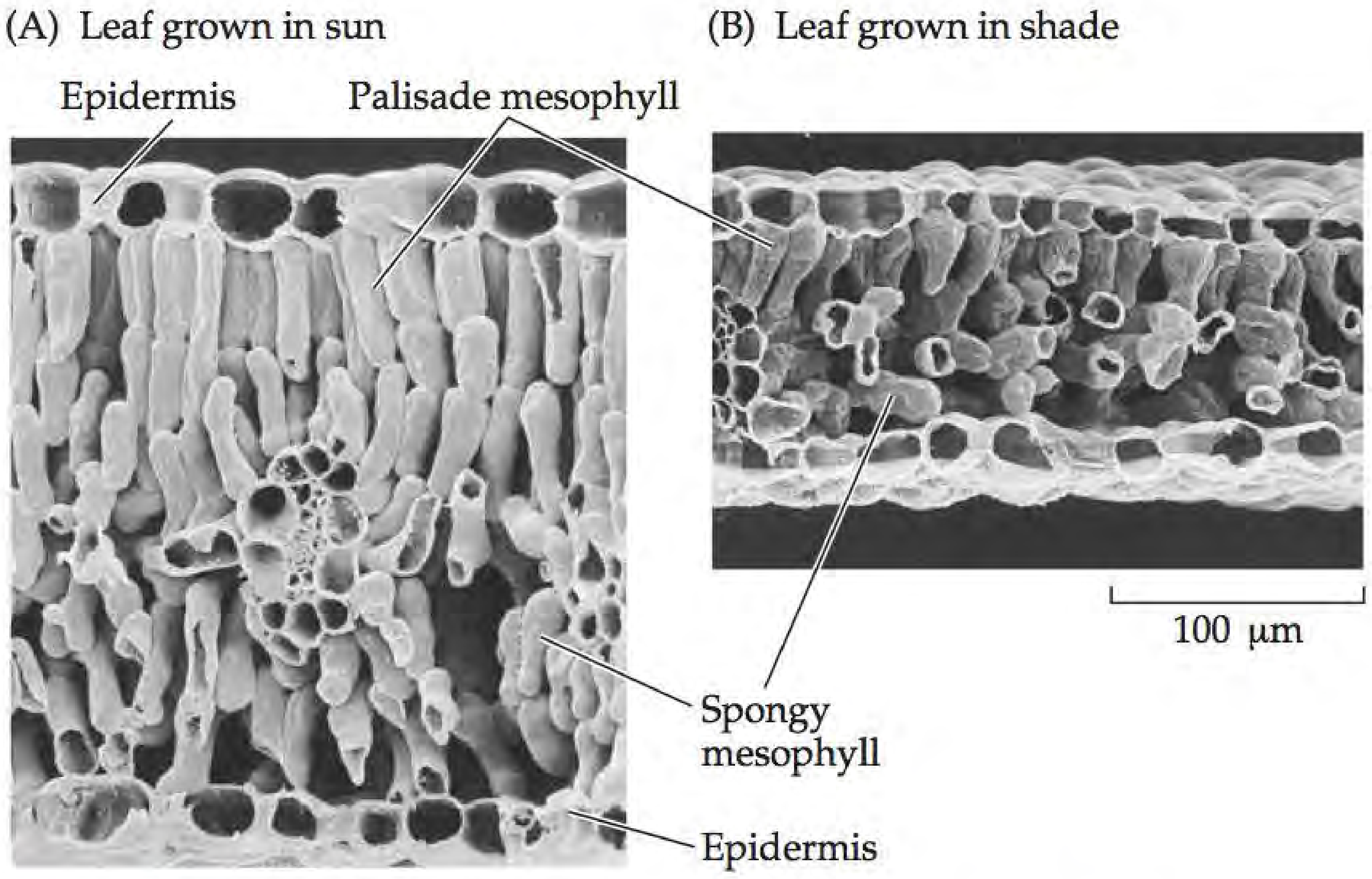
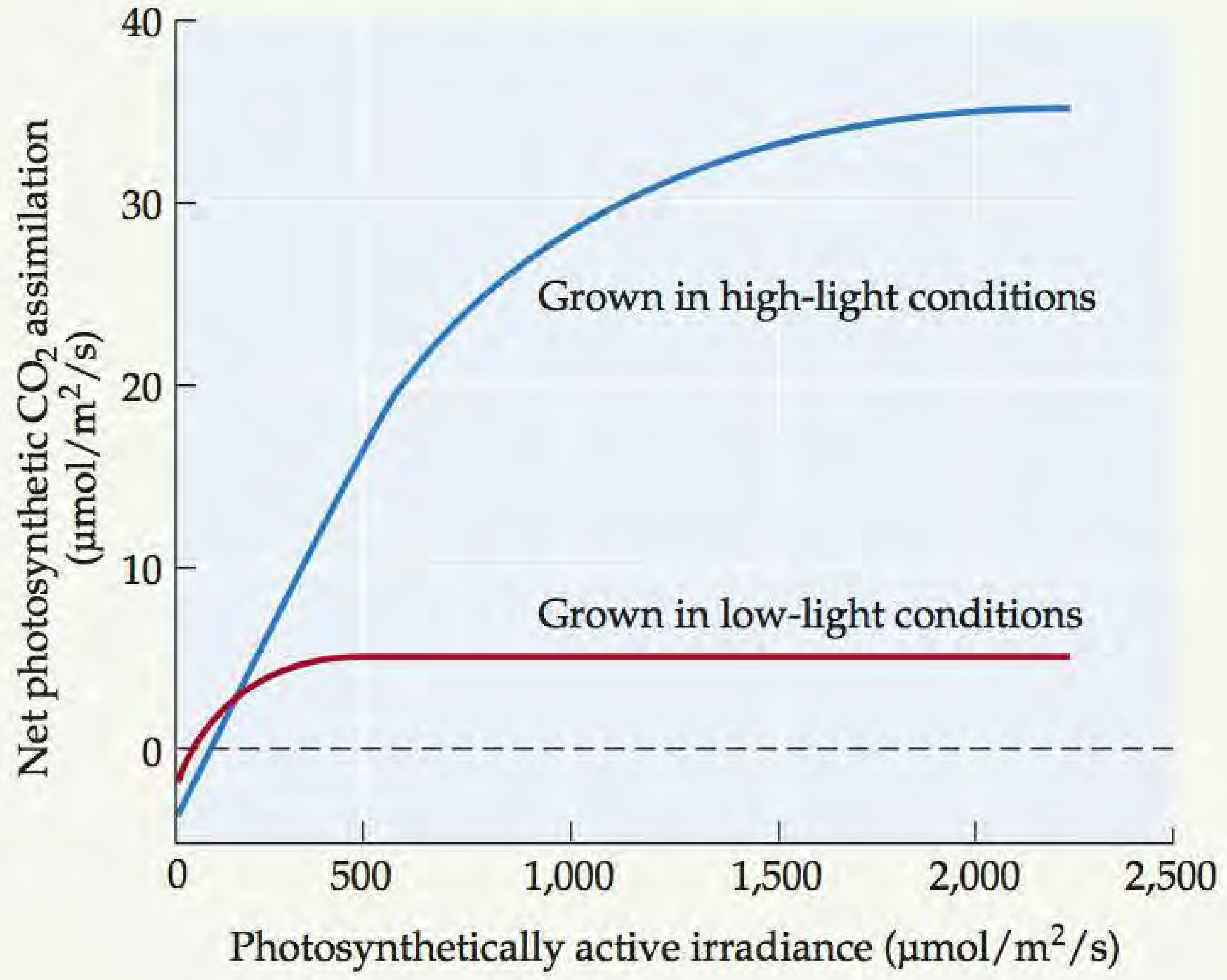


Figure 5.8 Effects of Light Level on Leaf Structure Golden banner (*Thermopsis montana*) leaves adjust morphologically to changes in light levels. Leaves grown at high light levels (A) are thicker, have more photosynthetic cells (palisade and spongy mesophyll), and have greater numbers of chloroplasts than leaves grown at low light levels (B). (Courtesy of T. Vogelmann.)

ANALYZING DATA 5.1 How Does Acclimatization Affect Plant Energy Balance?

Many plants can adjust their morphology and biochemistry to match the light conditions under which they are grown. The curves depicted in the figure are from Olle Björkman's* classic studies and show the net photosynthetic CO_2 uptake for spearscale plants (*Atriplex triangularis*) grown under high-light (920 μmol/m^2/s of photosynthetically active radiation) and low-light (92 μmol/m^2/s) conditions.



1. Assuming no further physiological changes occur, calculate the daily carbon balance for leaves of the high-light and low-light plants grown under the following conditions:
   - a. Plants are kept at a light level (irradiance) of 200 μmol/m^2/s for 2 hours, then switched to an irradiance of 1,500 μmol/m^2/s for 10 hours, then switched back to 200 μmol/m^2/s for 2 hours. The lights are then turned off for 10 hours. (This light regime approximates sunny conditions in an open subtropical savanna.)
   - b. Plants are kept at an irradiance of 50 μmol/m^2/s for 2 hours, then switched to an irradiance of 200 μmol/m^2/s for 10 hours, then switched back to 50 μmol/m^2/s for 2 hours. The lights are then turned off for 10 hours. (This light regime is similar to that expected in a tropical rainforest understory.)
2. High-light and low-light plants exhibit differences in maximum net photosynthesis rates, light compensation points, and nighttime respiration. Which of these three differences contributes the most to the distinction in carbon balance under high-light conditions (calculated in part a of question 1) and low-light conditions (calculated in part b)?
3. What do you think might contribute to the differences in nighttime respiration rates?

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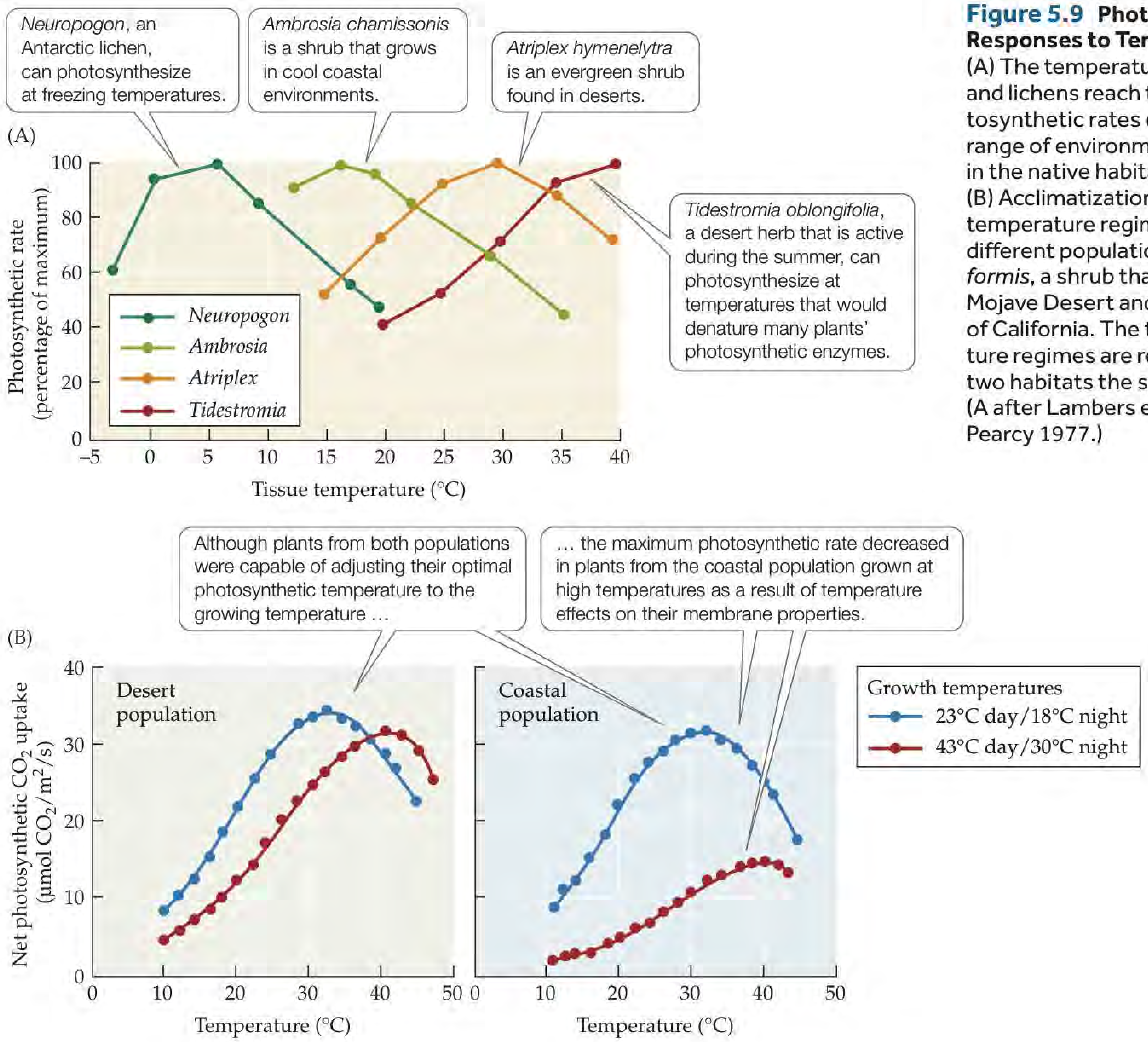
*Björkman, O. 1981. Responses to different quantum flux densities. In *Physiological Plant Ecology I: Encyclopedia of Plant Physiology*, O. L. Lange et al. (eds.). 57–101. Springer-Verlag, Berlin.

See the companion website for a similar ANALYZING DATA exercise.

cycle is not operating, energy continues to accumulate in the light-harvesting arrays, and if enough energy builds up, it can damage the photosynthetic membranes. Plants have evolved a number of ways of dissipating this energy safely, including the use of carotenoids to release it as heat, as described in **Web Extension 5.1**.

Temperature influences photosynthesis in two main ways: through its effects on the rates of chemical reactions and by influencing the structural integrity of membranes and enzymes. Autotrophs acclimatize and adapt to temperature variation by changing properties of the Calvin cycle enzymes and/or the photosynthetic membranes. Different photosynthetic organisms have different forms of the same photosynthetic enzymes that operate best under the environmental temperatures where the organisms occur. These differences result in markedly different temperature ranges for photosynthesis in organisms from different climates (**Figure 5.9A**). Lichens and plants of Arctic and alpine environments can photosynthesize at temperatures close to freezing, while desert plants may have their highest photosynthetic rates at temperatures that are hot enough to denature most other plants' enzymes (40°C–50°C or 104°F–122°F). Plants that acclimatize to changes in temperature synthesize different forms of photosynthetic enzymes with different temperature optima (**Figure 5.9B**). Temperature also influences the fluidity of the cell and organelle membranes (see Concept 4.2). Cold sensitivity in plants of tropical and subtropical biomes is associated with loss of membrane fluidity, which inhibits the functioning of the light-harvesting molecules embedded in the chloroplast membranes. And as we have seen, high temperatures, particularly in combination with intense sunlight, can damage photosynthetic membranes.

Nutrient concentrations in leaves reflect their photosynthetic potential because most of the nitrogen in plants



Neuropogon, an Antarctic lichen, can photosynthesize at freezing temperatures.

Ambrosia chamissonis is a shrub that grows in cool coastal environments.

Atriplex hymenelytra is an evergreen shrub found in deserts.

Tidestromia oblongifolia, a desert herb that is active during the summer, can photosynthesize at temperatures that would denature many plants' photosynthetic enzymes.

Although plants from both populations were capable of adjusting their optimal photosynthetic temperature to the growing temperature …

… the maximum photosynthetic rate decreased in plants from the coastal population grown at high temperatures as a result of temperature effects on their membrane properties.

Figure 5.9 Photosynthetic Responses to Temperature (A) The temperatures at which plants and lichens reach their maximum photosynthetic rates correspond to the range of environmental temperatures in the native habitat of the species. (B) Acclimatization to different growth temperature regimes by plants from different populations of *Atriplex lentiformis*, a shrub that occurs in the hot Mojave Desert and in cool coastal zones of California. The two growth temperature regimes are representative of the two habitats the species occupies. (A after Lambers et al. 1998; B after Pearcy 1977.)

is associated with rubisco and other photosynthetic enzymes. Thus, higher amounts of nitrogen in leaves are correlated with higher photosynthetic rates. Why, then, don't all plants allocate more nitrogen to their leaves to increase their photosynthetic capacity? There are two main reasons. First, the supply of nitrogen is low relative to the demand, and nitrogen is needed for growth and other metabolic functions in addition to photosynthesis (see Chapter 22). Second, increasing the nitrogen concentration of a leaf increases the risk that herbivores will consume the leaf, as plant-eating animals are often nitrogen starved (see Concept 22.1). Plants must balance the competing demands of photosynthesis, growth, and protection from herbivores.

Over evolutionary time, some plants have dealt with environmental constraints on photosynthesis with adaptations in their photosynthetic pathways, as we will see next.

CONCEPT 5.3

Environmental constraints have resulted in the evolution of biochemical pathways that improve the efficiency of photosynthesis.

Photosynthetic Pathways

Anything that influences energy gain by photosynthesis has the potential to affect the survival, growth, and reproduction of the organism. As we have just seen, rates of photosynthesis are influenced by environmental conditions, particularly temperature and water availability. In addition, an apparent biochemical inefficiency in the initial step of the Calvin cycle limits energy gain by photosynthetic organisms. In this section, we will examine some evolutionary responses to these environmental constraints on photosynthesis. We will describe two specialized photosynthetic pathways, the C_4 pathway and crassulacean acid metabolism (CAM), that make photosynthesis more efficient under particular potentially stressful environmental conditions. Plants that lack these specialized pathways use the **C_3 photosynthetic pathway**. The C_3 and C_4 photosynthetic pathways take their names from the number of carbon atoms in their first stable chemical products. First, we'll examine photorespiration, a process that operates in opposition to the Calvin cycle and lowers its efficiency.

Photorespiration lowers the efficiency of photosynthesis

Earlier, we described a key enzyme in the Calvin cycle, rubisco, and noted that the "o" in the abbreviation stands for "oxygenase." Rubisco can catalyze two competing reactions. One is a carboxylase reaction, in which CO_2 is taken up, leading to the synthesis of sugars and the release of O_2 (i.e., photosynthesis; see Equation 5.1). The other is an oxygenase reaction, in which O_2 is taken up, leading to the breakdown of carbon compounds and the release of CO_2. This oxygenase reaction is part of a process called **photorespiration**, which results in a net loss of energy and is thus potentially detrimental for plants.

The balance between photosynthesis and photorespiration is related to two main factors: (1) the ratio of O_2 to CO_2 in the atmosphere and (2) temperature. As the atmospheric concentration of CO_2 decreases relative to that of O_2, the rate of photorespiration increases relative to the rate of photosynthesis (**Figure 5.10**). Since the evolution of C_3 photosynthesis over 3 billion years ago, atmospheric CO_2 concentrations have changed repeatedly over periods of hundreds of thousands of years in response to major global geologic and climate events (see Concepts 25.1 and 25.2). These shifts in atmospheric CO_2 concentrations would have influenced the balance between photosynthesis and photorespiration. Furthermore, as temperatures increase, the rate of O_2 uptake catalyzed by rubisco increases relative to the rate of CO_2 uptake, and the solubility of CO_2 in the cytoplasm decreases more than that of O_2. As a result of these two processes, photorespiration increases more rapidly at high temperatures than photosynthesis does. Thus, energy loss due to photorespiration is particularly acute at high temperatures and low atmospheric CO_2 concentrations.

If photorespiration is detrimental to the functioning of photosynthetic organisms, why hasn't a new form of rubisco evolved that minimizes uptake of O_2? Is it possible that photorespiration provides some benefit to the plant? A possible clue comes from experiments with *Arabidopsis thaliana*. *Arabidopsis* plants with a genetic mutation that knocks out photorespiration die under normal light and CO_2 conditions (Ogren 1984). One hypothesis for a potential benefit of photorespiration is that it protects the plant from damage to the photosynthetic machinery at high light levels. This hypothesis is supported by the results of a study by Akiko Kozaki and Go Takeba, who used tobacco plants (*Nicotiana* sp.) that they genetically altered to elevate or lower the plants' rates of photorespiration (Kozaki and Takeba 1996). They subjected these experimental plants to high-intensity light and recorded the damage to their photosynthetic machinery. Plants with higher rates of photorespiration showed less damage than control plants with normal rates of photorespiration (**Figure 5.11**) or plants with depressed rates of photorespiration.

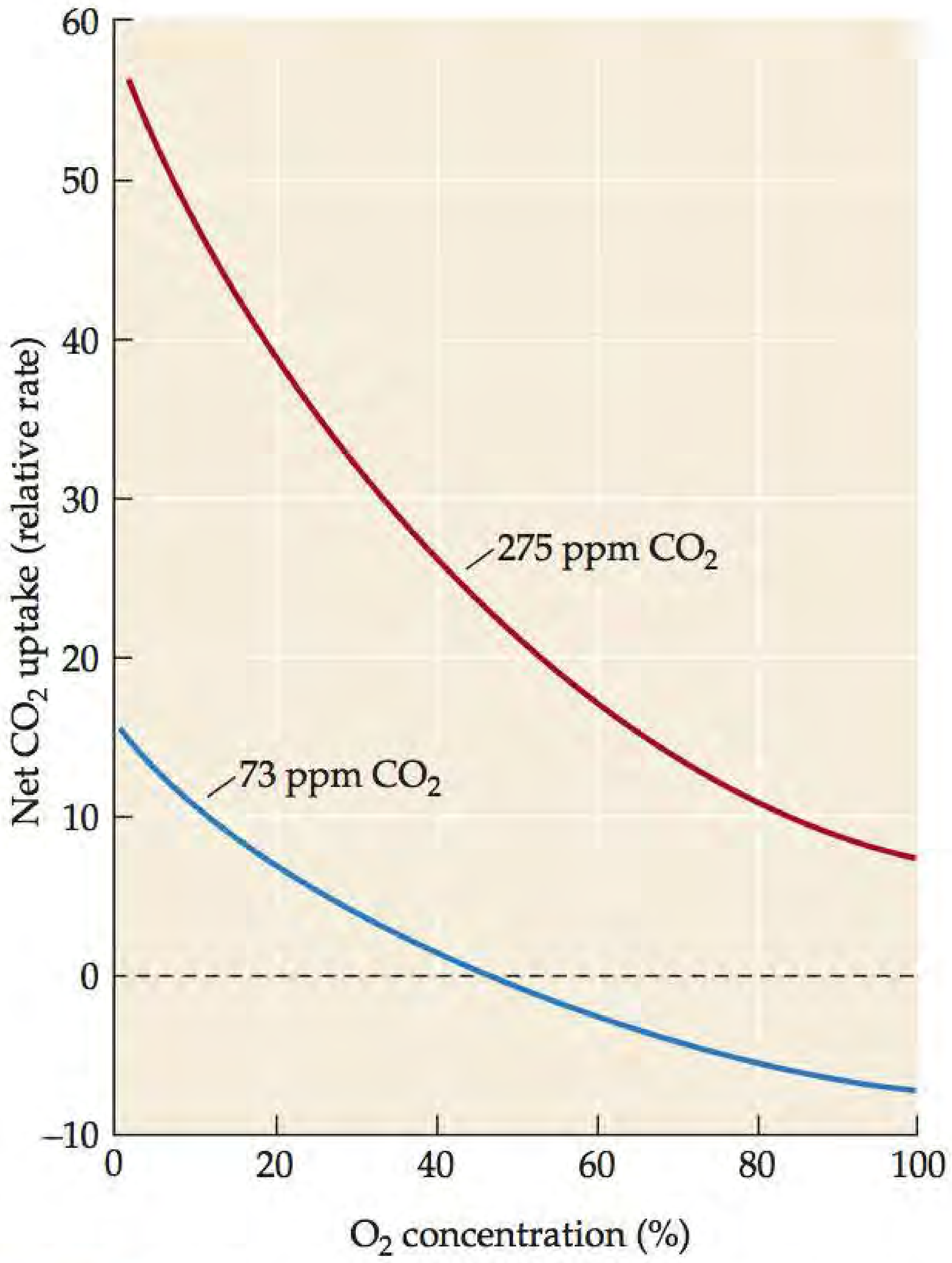


Figure 5.10 Influence of Oxygen Concentration on Photosynthesis As the atmospheric oxygen concentration increases, net photosynthetic uptake of CO_2 decreases because of greater photorespiration, as shown here for soybean leaves in light levels equal to about 20% of full sun. (After Forrester et al. 1966.)

? Why does the net rate of CO_2 uptake drop below zero at high oxygen levels for leaves exposed to 73 ppm CO_2?

Despite this possibility that photorespiration plays a role in protecting plants from damage at high light levels, there are conditions in which the decrease in photosynthetic CO_2 uptake it causes could be a serious problem for the plant. If atmospheric CO_2 concentrations are low and temperatures high, photosynthetic energy gain might not keep pace with photorespiratory energy loss. Such conditions existed 7 million years ago, at about the time when plants with a unique biochemical pathway,

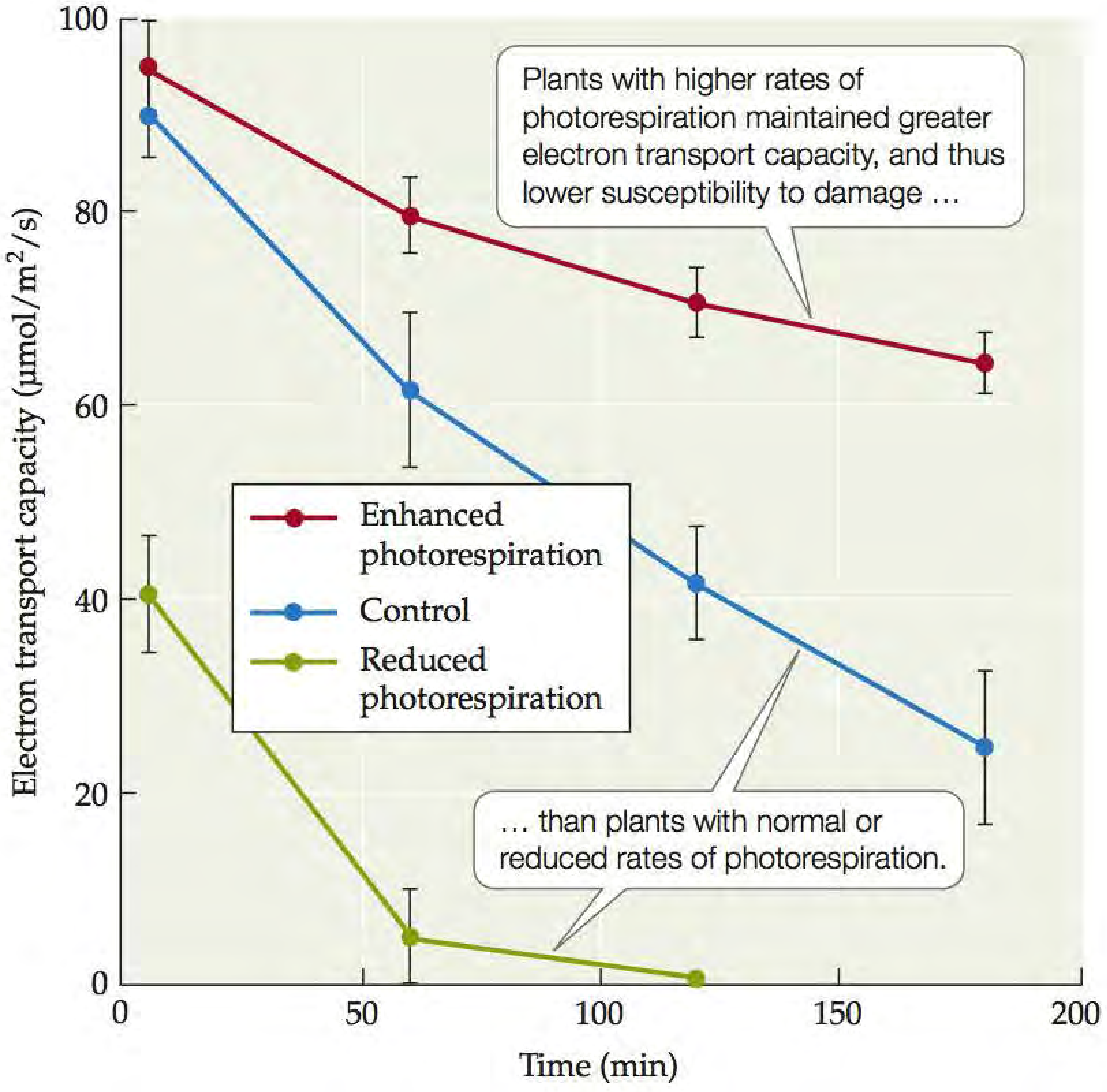


Figure 5.11 Does Photorespiration Protect Plants from Damage by Intense Light? The ability of plants to process light energy for photosynthesis (electron transport capacity) under conditions that promote damage to photosynthetic membranes (high light levels, low CO_2 concentrations) is greater in genetically altered plants with high rates of photorespiration than in control plants or in genetically altered plants with low rates of photorespiration. Error bars show ± one SE of the mean. (After Kozaki and Takeba 1996.)

C_4 photosynthesis, became far more abundant (Cerling et al. 1997).

C_4 photosynthesis lowers photorespiratory energy loss

The **C_4 photosynthetic pathway** reduces photorespiration. C_4 photosynthesis evolved independently several times in different plant species. It is found in 18 plant families (**Figure 5.12**), but is most closely associated with the grass family. Well-known examples of crop plants with the C_4 pathway include corn, sugarcane, and sorghum.

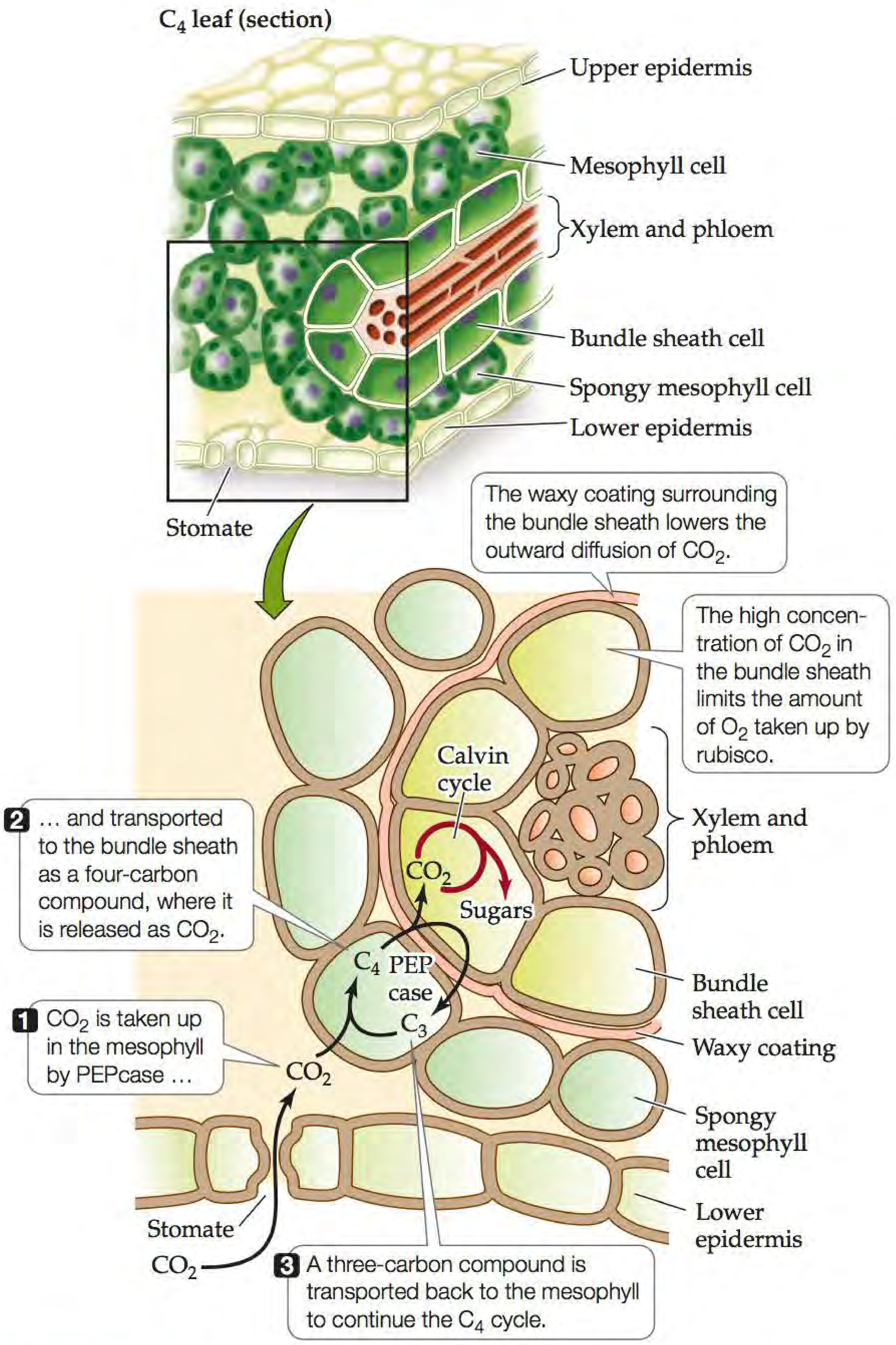
C_4 photosynthesis involves both biochemical and morphological specialization. The biochemical specialization can be thought of as a pump that provides high concentrations of CO_2 to the Calvin cycle. This greater supply of CO_2 lowers the rate of O_2 uptake by rubisco, substantially reducing photorespiration. The morphological specialization involves spatial separation of the regions in the leaf where CO_2 is taken up (mesophyll) and where the Calvin cycle operates (bundle sheath), which increases the concentration of CO_2 where rubisco is found.


(A) Corn (*Zea mays*)

(B) *Haloxylon ammodendron*

Figure 5.12 Plants with the C_4 Photosynthetic Pathway The C_4 photosynthetic pathway has evolved multiple times. It is found in plants of 18 different families encompassing a variety of growth forms, from monocot grasses such as sugarcane and corn (A) to eudicots such as this saxaul tree in the Charyn Canyon in Kazakhstan (B).

In C_4 plants, CO_2 is initially taken up by an enzyme called phosphoenolpyruvate carboxylase, or PEPcase, that has a greater capacity to take up CO_2 than rubisco and lacks oxygenase activity. PEPcase fixes CO_2 in the mesophyll tissue of the plant. Once the CO_2 is taken up, a four-carbon compound is synthesized and transported to a group of cells surrounding the vascular tissues (xylem and phloem), known as the bundle sheath, where the Calvin cycle occurs. The four-carbon compound is broken down in the bundle sheath cells, releasing CO_2 to the Calvin cycle, and a three-carbon compound is transported back to the mesophyll to continue the C_4 cycle. The bundle sheath is surrounded by a waxy coating that keeps CO_2 from diffusing out (**Figure 5.13**). As a result, CO_2 concentrations inside the bundle sheath may reach a high of 5,000 parts per million (ppm), even though external CO_2 concentrations are only 404 ppm. Additional energy in the form of ATP must be expended to operate the C_4 photosynthetic pathway, but the increased efficiency of carbon fixation compensates for the higher energy requirement.



The waxy coating surrounding the bundle sheath lowers the outward diffusion of CO_2.

The high concentration of CO_2 in the bundle sheath limits the amount of O_2 taken up by rubisco.

1 CO_2 is taken up in the mesophyll by PEPcase ...

2 ... and transported to the bundle sheath as a four-carbon compound, where it is released as CO_2.

3 A three-carbon compound is transported back to the mesophyll to continue the C_4 cycle.

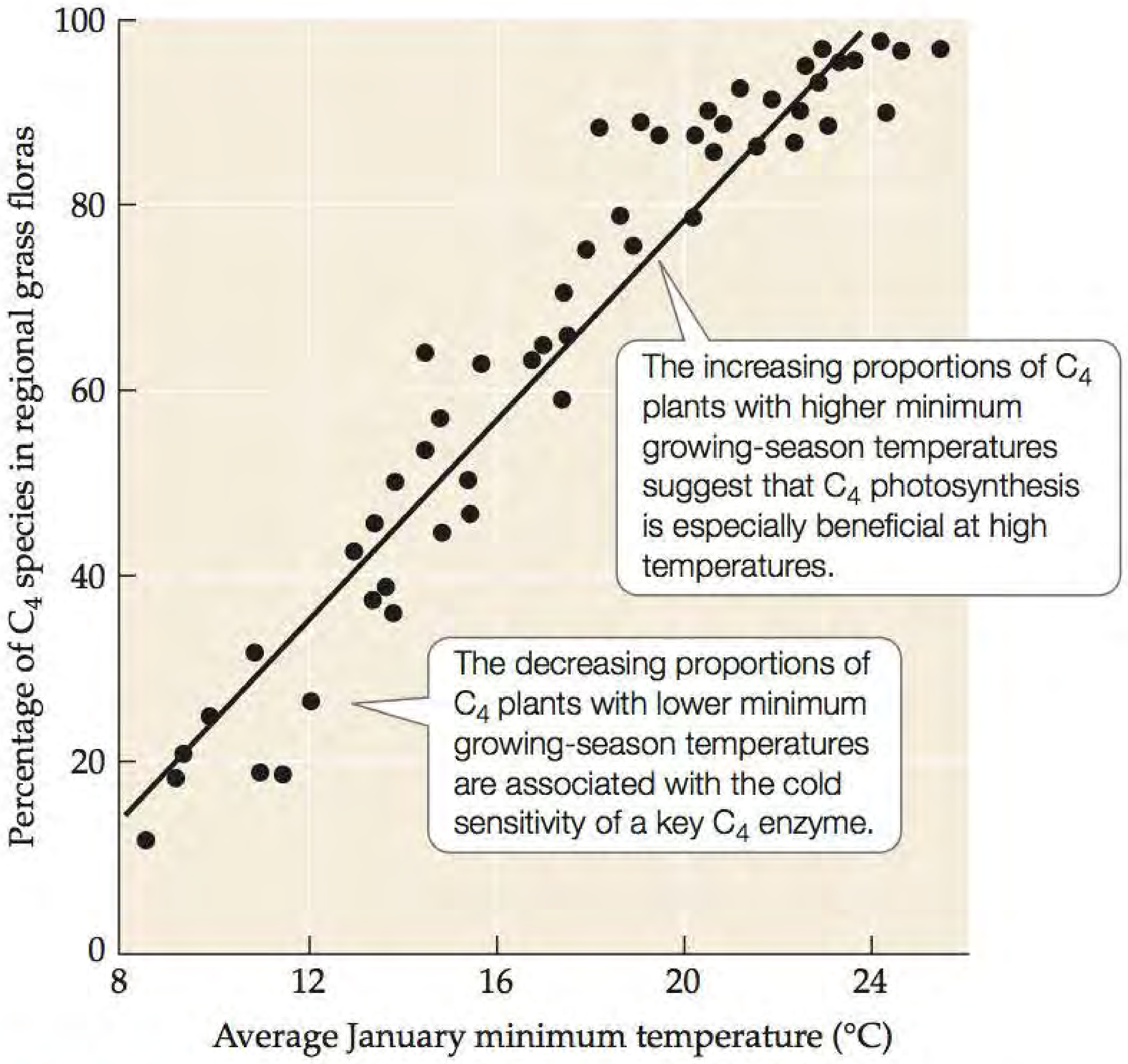
Figure 5.13 Morphological Specialization in the Leaves of C_4 Plants The spatial separation of CO_2 uptake (in the mesophyll cells) and the Calvin cycle (in the bundle sheath cells) minimizes photorespiration and maximizes photosynthetic rates under high temperatures.

As is apparent from the discussion above, plants with the C_4 photosynthetic pathway can photosynthesize at higher rates than C_3 plants under environmental conditions that elevate rates of photorespiration, such as high temperatures. In addition, most C_4 plants have lower rates of transpiration at a given photosynthetic rate, known as *water use efficiency*, than C_3 plants. This difference is due to the ability of PEPcase to take up CO_2 under the lower CO_2 concentrations that exist when stomates are not fully open.

If we assumed that photosynthetic rates determine ecological success, we could use climate patterns to predict where C_4 plants should predominate over C_3 plants. Such an analysis would be overly simplistic, however, because multiple factors other than temperature influence the biogeography of C_3 and C_4 plants, including abiotic factors such as light levels and biotic factors such as competitive ability and the pool of species available to colonize an area. However, analyses of similar communities across latitudinal and elevational gradients provide support for the benefit of C_4 photosynthesis at high temperatures and for the role this benefit plays in C_4 plant distribution (Ehleringer et al. 1997). In particular, studies of grass- and sedge-dominated communities in Australia suggest a close correlation between growing-season temperature and the proportion of C_3 and C_4 species in the community (**Figure 5.14**). As atmospheric CO_2 concentrations continue to increase because of burning of fossil fuels, however, photorespiration rates are likely to decrease, and the advantages of C_4 over C_3 photosynthesis may be diminished in some regions, leading to changes in the proportions of C_3 and C_4 plants.

CAM photosynthesis enhances water conservation

When plants first colonized the terrestrial environment, they evolved adaptations to restrict water losses to a dry atmosphere. Among these adaptations is a unique photosynthetic pathway called **crassulacean acid metabolism** (**CAM**), which occurs in over 10,000 plant species belonging to 33 families. While C_4 photosynthesis separates CO_2 uptake and the Calvin cycle spatially, CAM separates these two steps temporally (**Figure 5.15**). CAM plants open their stomates at night, when C_3 and C_4 plants have their stomates closed. Because air temperatures at night are cooler, humidity is higher. Higher humidity results in a lower water potential gradient between the leaf and the air (see Concept 4.3), so the plant loses less water by transpiration than it would during the day. CAM plants close their stomates during the day, when the potential for water loss is highest.



The increasing proportions of C_4 plants with higher minimum growing-season temperatures suggest that C_4 photosynthesis is especially beneficial at high temperatures.

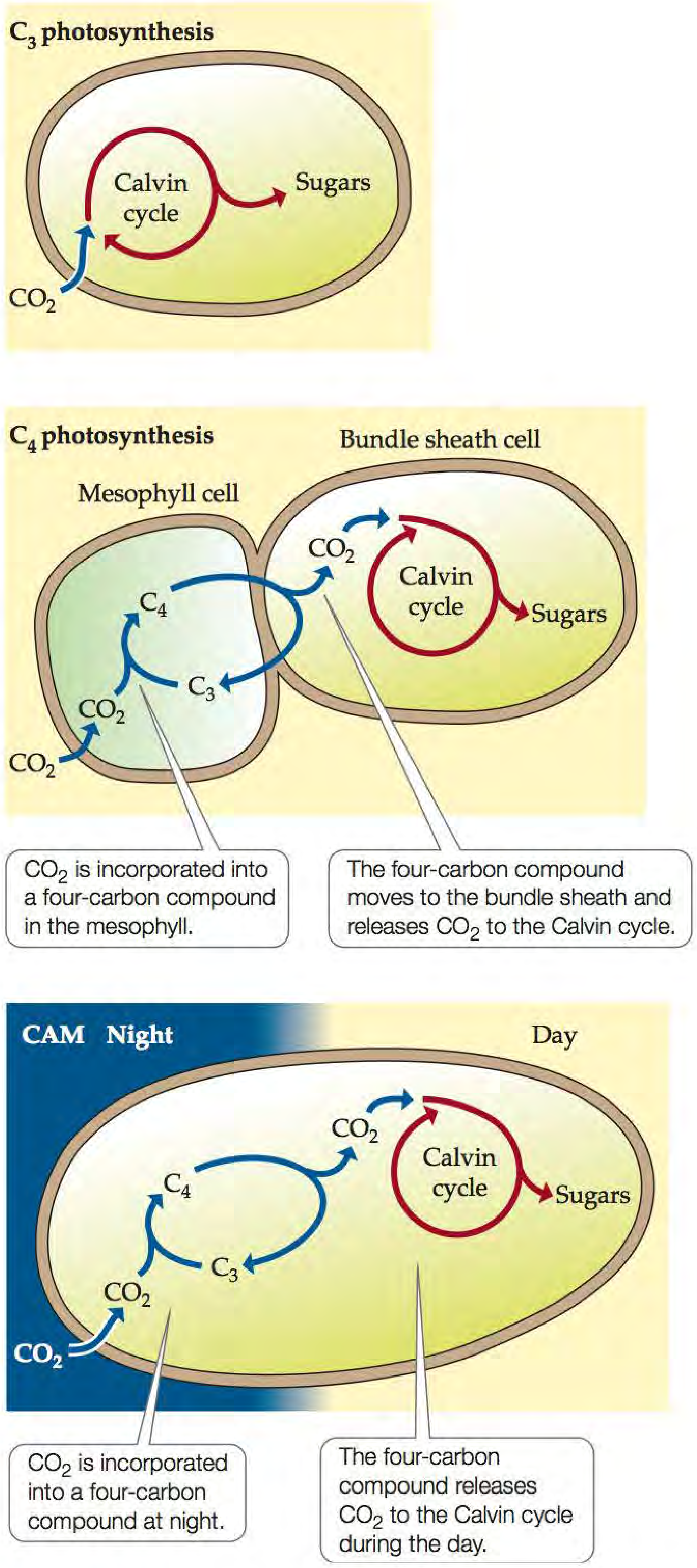
The decreasing proportions of C_4 plants with lower minimum growing-season temperatures are associated with the cold sensitivity of a key C_4 enzyme.

Figure 5.14 C_4 Plant Abundance and Growing-Season Temperatures The proportions of C_4 plants in Australian grass- and sedge-dominated communities correlate with the average minimum growing-season temperatures in the different locations. (After Henderson et al. 1995.)

Using the data in this graph and the seasonal temperature trends from the climate diagrams in Concept 3.1 (assume that the monthly minimum temperature is 5°C cooler than the monthly average), what biome(s) should lack C_4 species?

During the night, when the stomates are open, CAM plants take up CO_2 using PEPcase and incorporate it into a four-carbon organic acid, which is stored in vacuoles (**Figure 5.16**). The resulting increase in acidity in the plants' tissues during the night is characteristic of CAM plants and can be used to estimate their photosynthetic rates. During the day, when the stomates are closed, the organic acid is broken down, releasing CO_2 to the Calvin cycle. CO_2 concentrations in the photosynthetic tissues of CAM plants are thus higher than those in the atmosphere during the day. These high CO_2 concentrations increase the efficiency of photosynthesis as they suppress photorespiration. Photosynthetic rates in CAM plants are usually related to the capacity of the plant to store the four-carbon organic acid, so many CAM plants are *succulent*, with thick, fleshy leaves or stems, which enhances their nighttime acid storage capacity.

CAM plants are typically associated with arid and saline environments, such as deserts and Mediterranean-type ecosystems (**Figure 5.17**). Some CAM plants, however, are found in the humid tropics. Tropical CAM plants are typically epiphytes growing on the branches of trees, without access to the abundant water stored in the soil. These epiphytes rely on rainfall for their water supply and may be subject to long periods without access to water.



CO_2 is incorporated into a four-carbon compound in the mesophyll.

The four-carbon compound moves to the bundle sheath and releases CO_2 to the Calvin cycle.

CO_2 is incorporated into a four-carbon compound at night.

The four-carbon compound releases CO_2 to the Calvin cycle during the day.

Figure 5.15 C_3, C_4, and CAM Photosynthesis Compared All three photosynthetic pathways fix carbon and produce sugars, but C_4 photosynthesis separates these steps spatially, while CAM separates them temporally.

The CAM pathway is also found in some aquatic plants, such as quillworts (*Isoetes*), which are closely related to the club mosses. This observation suggests that water conservation was probably not the only driving force for the evolution of CAM, which evolved independently

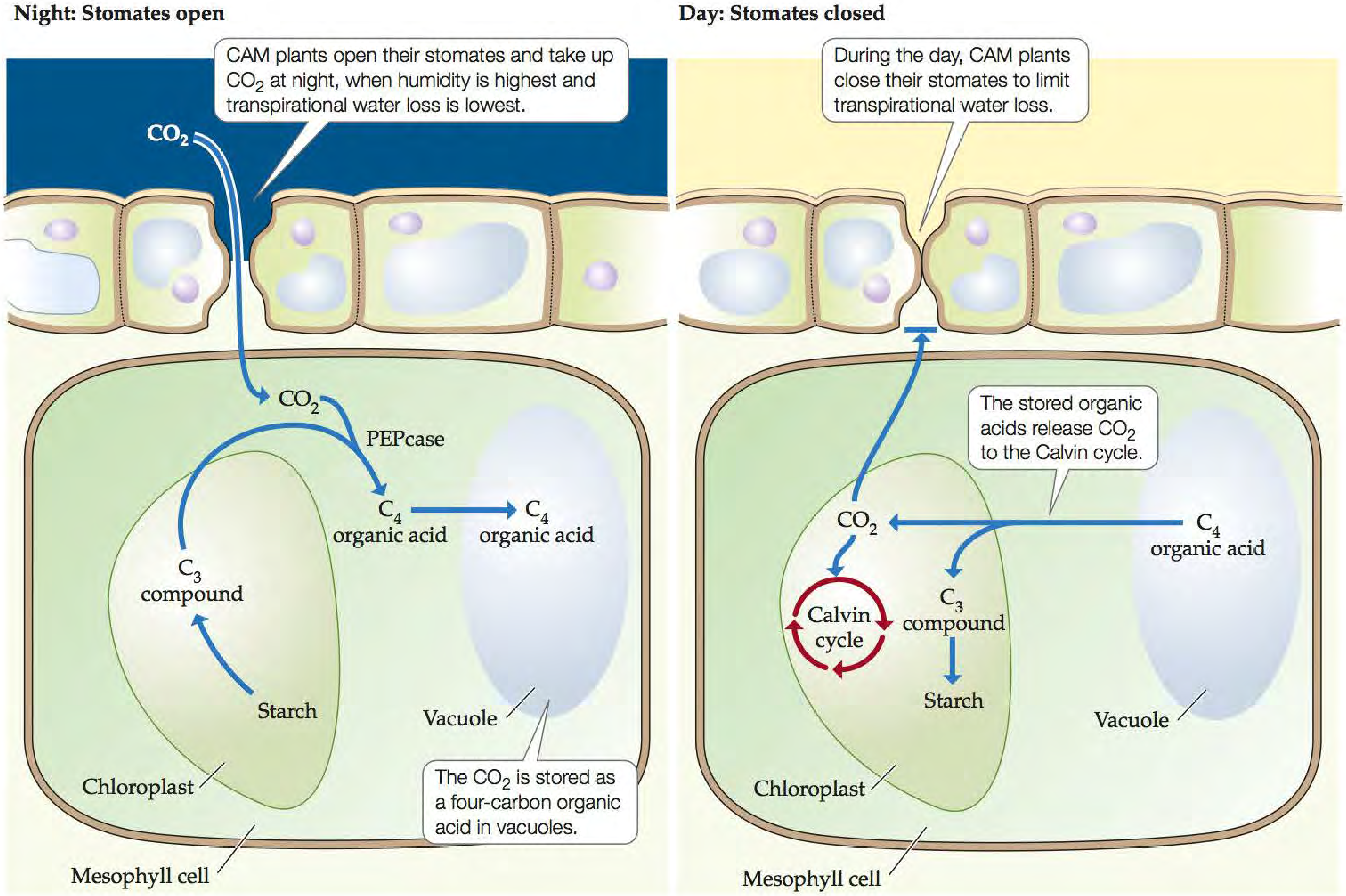


Figure 5.16 **Crassulacean Acid Metabolism** Plants using CAM open their stomates and take up CO_2 at night, then run the Calvin cycle during the day.


Crassula sp.

Ferocactus sp.

Pineapple (*Ananas comosus*)

Figure 5.17 **Examples of Plants with the CAM Photosynthetic Pathway** Most CAM plants are found in arid and saline regions or in other habitats where water availability is periodically low.

in several different plant groups. The rate of CO_2 diffusion into water is low, and CAM has been hypothesized to facilitate the uptake of CO_2 at the low concentrations found in the aquatic environment.

A unique property of some CAM plant species is the ability to switch between C_3 and CAM photosynthesis, known as *facultative CAM*. When conditions are favorable for daytime gas exchange (i.e., abundant water is available), these plants utilize the C_3 photosynthetic pathway, which allows greater carbon gain than CAM. As conditions become more arid or more saline, the plants switch over to CAM. The reversibility of the transition from C_3 to CAM varies among species. For example, the common ice plant (*Mesembryanthemum crystallinum*), which has been intensively studied as a facultative CAM model system, undergoes an irreversible transition from C_3 to CAM photosynthesis when salinity increases or the soil dries out (Osmond et al. 1982). In contrast, some species in the genus *Clusia* can switch relatively rapidly between C_3 and CAM (Borland et al. 1992). These plants start out as epiphytes in canopy trees but grow toward the base of their host tree, eventually strangling it and taking on a tree growth form. The capacity to switch between C_3 and CAM facilitates the change from epiphyte to tree form, and it supports continued photosynthesis during the transition from wet season to dry season characteristic of some tropical locations.

How can we tell what photosynthetic pathway a plant is using? The morphology of the plant gives us a clue: succulent plants suggest CAM photosynthesis, and plants with a well-developed bundle sheath suggest C_4 photosynthesis. These clues provide a starting point, but they are far from foolproof. We can measure the presence and activity of specific enzymes, but this approach requires substantial sample preparation and laboratory time. A simpler approach is to measure the ratio of stable carbon isotopes ($^{13}C/^{12}C$) in plant tissues. Although the isotopic technique uses sophisticated equipment, sample preparation is simple, and there are numerous laboratories that can routinely analyze plant tissue samples (see **Ecological Toolkit 5.1**).

Now that we have reviewed the ways in which autotrophs acquire energy, let's turn our attention to how that energy is acquired by heterotrophs.

CONCEPT 5.4

Heterotrophs have adaptations for acquiring and assimilating energy efficiently from a variety of organic sources.

Heterotrophy

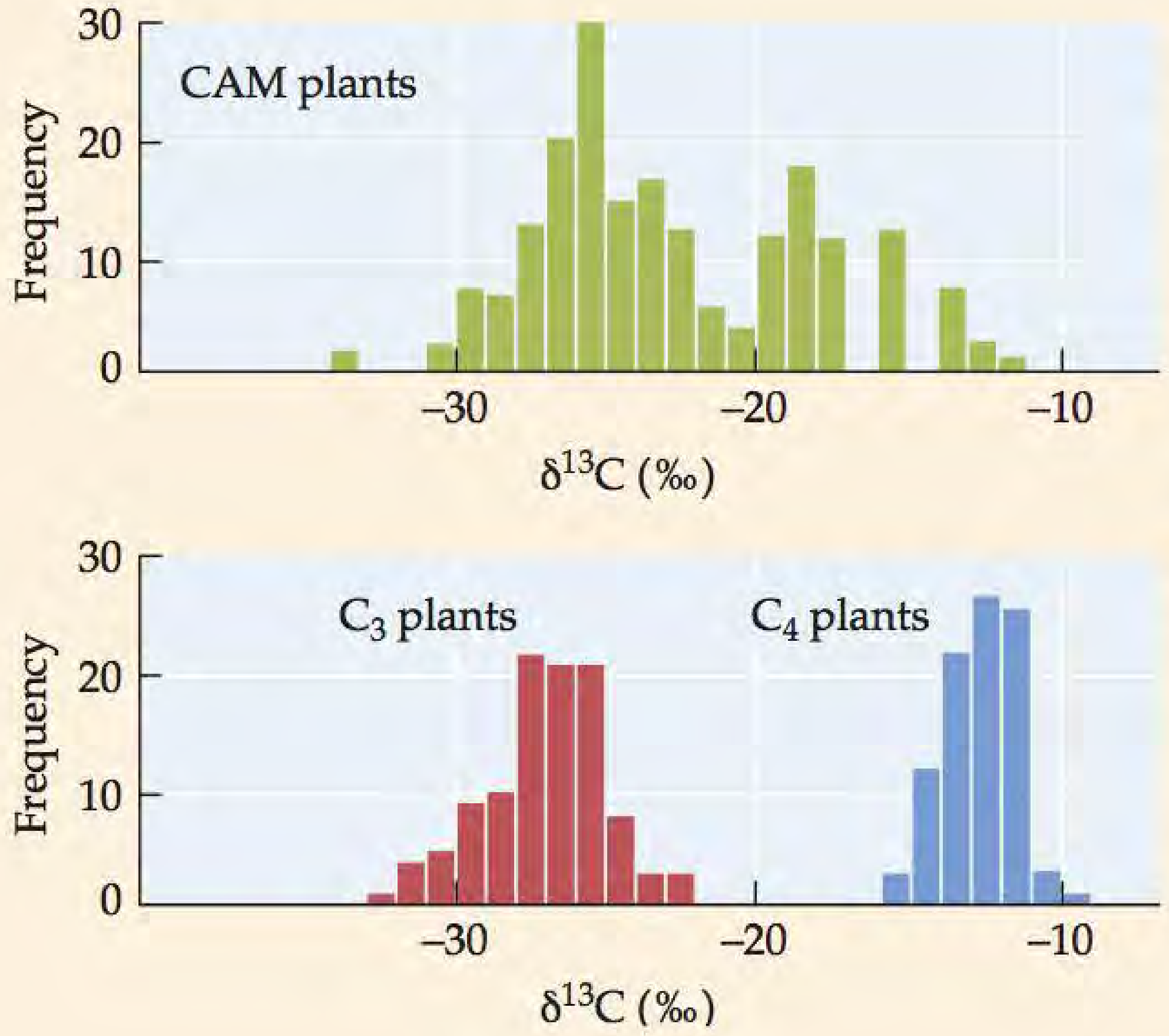
Heterotrophy is all about eating and being eaten, which are major themes in ecology. The first organisms on Earth were probably heterotrophs that consumed amino acids and sugars, which formed spontaneously in the early atmosphere and rained down on the surface or formed in the oceans near hydrothermal vents. Since that time, the diversity of strategies for obtaining energy by heterotrophs has expanded tremendously. Three general steps are associated with heterotrophic energy acquisition: finding and obtaining food, consuming food, and absorbing its energy and nutrients. The organic matter that provides energy for heterotrophs includes living and freshly killed organisms as well as **detritus**—organic material derived from dead organisms in various stages of decomposition (see Concept 20.4). In this section, we will examine food sources, the ways in which heterotrophs obtain energy, and factors that influence absorption of food. There is a wide range of variation in the complexity of heterotrophic energy acquisition and assimilation processes that is associated with heterotroph body size and physiology. In Chapters 12 and 13, we will take a more in-depth look at the various types of consumers (predators, herbivores, and parasites), and we will see how the food they consume affects their growth and reproduction as well as the distributions and abundances of both the consumers themselves and their food resources (prey and hosts).

Food sources differ in their chemistry and availability

Heterotrophs consume energy-rich organic compounds (food) from their environment and convert them into usable chemical energy—primarily ATP—by processes such as *glycolysis*, which breaks down carbohydrates. The heterotroph's energy gain from food depends on the chemistry of the food, which determines its digestibility and its energy content. The effort invested in finding and obtaining the food also influences how much benefit the heterotroph gets from consuming it. For example, microorganisms that consume detritus in the soil invest little energy in obtaining food. However, the energy content of this decomposing plant matter is low compared with the energy content of live organisms. Living prey are rarer than detritus, and they may have defensive mechanisms that their predators must expend energy to overcome. Thus, a cheetah hunting a gazelle invests substantial energy in finding, chasing, capturing, and killing its prey, but it obtains a substantial, energy-rich meal if the hunt is successful.

The benefit of a food source to a heterotroph is partly related to the chemical compounds that the food contains. The chemical constituents of food can be placed into several categories based on their energy content and ease of assimilation (**Figure 5.18**). While water can be an important part of an animal's food, as we saw in Concept 4.3, it does not provide energy. The energy in food is found

ECOLOGICAL TOOLKIT 5.1 Stable Isotopes



Carbon Isotopic Composition of Plants with Different Photosynthetic Pathways Plants with the C_3 photosynthetic pathway show the greatest discrimination against ^{13}C (and thus the most negative $\delta\,^{13}C$, expressed in parts per thousand), while C_4 and CAM plants are more enriched in ^{13}C (have a less negative $\delta\,^{13}C$). (After Maslin and Thomas 2003.)

? Why is the range of $\delta\,^{13}C$ values for CAM plants larger, bridging the values for C_3 and C_4 plants?

Many biologically important elements, including carbon, hydrogen, oxygen, nitrogen, and sulfur, have an abundant "light" isotopic form and one or more "heavy" nonradioactive isotopic forms, which contain additional neutrons. Because isotopes of these elements do not decay over time as radioactive isotopes do, they are referred to as stable isotopes. An example of a stable isotope is carbon-13 (^{13}C), which is heavier than the more abundant form, carbon-12 (^{12}C), because it has one more neutron. Groups of stable isotopes include hydrogen (H) and deuterium (D or ^{2}H); nitrogen-14 and nitrogen-15 (^{14}N and ^{15}N); and oxygen-16, oxygen-17, and oxygen-18 (^{16}O, ^{17}O, and ^{18}O). The lighter isotopes of these elements are much more abundant than the heavier forms. For example, ^{12}C constitutes 98.9%, and ^{13}C only 1.1%, of the C on Earth. Similarly, ^{14}N constitutes 99.6%, and ^{15}N 0.4%, of the N on Earth.

The isotopic composition of a material is usually expressed as delta (δ), the difference between the ratio of the isotopic forms in a sample (R_{sample}) and that in a standard material (R_{standard}), divided by the ratio in the standard, multiplied by 1,000 [to give parts per thousand (‰) difference]:

$$\delta = \frac{R_{\text{sample}} - R_{\text{standard}}}{R_{\text{standard}}} \times 1{,}000$$

Examples of the standard materials chosen for stable isotopes include a limestone rock from South Carolina for C, atmospheric N_2 for N, and ocean water for O and H.

Naturally occurring stable isotopes have become an important tool in ecological research (Fry 2007). Stable isotopes have been used to determine photosynthetic pathways in plants, identify food sources for animals, and track the movements of elements and rates of nutrient cycling in ecosystems. Because of differences in mass, the isotopes are affected differently by biological and physical processes. Generally, the heavier isotope is discriminated against and the lighter isotope enriched. For example, when rubisco catalyzes the uptake of CO_2, it favors $^{12}CO_2$ over $^{13}CO_2$. As a result, plants are enriched in ^{12}C, and depleted in ^{13}C, relative to the C in atmospheric CO_2: atmospheric CO_2 has a $\delta\,^{13}C$ value of –7 parts per thousand (in other words, it is 7 parts per thousand more depleted in ^{13}C than the standard), and C_3 plants have a $\delta\,^{13}C$ value of about –27 parts per thousand. C_4 and CAM plants, however, have less ^{12}C and more ^{13}C than C_3 plants. That is because initial CO_2 uptake in these plants is catalyzed by PEPcase, which discriminates against $^{13}CO_2$ less than rubisco does, and rubisco in C_4 and CAM plants takes up CO_2 in a semi-closed system (in the bundle sheath or with stomates closed), which inhibits enzymatic discrimination. As a result, measurement of the C isotope ratio in plant tissues can be used to determine the photosynthetic pathway used by a plant species, as shown in the figure.

Stable isotopes have also been used to determine food sources for animals. The isotopic ratios of C, N, and S in various potential food sources may differ significantly, and measurement of one or more of these isotopes in potential food sources and in consumer tissues can determine what is being eaten. For example, in this chapter's Case Study Revisited, we will see how isotopic ratios were used to determine the diet of New Caledonian crows. In Concept 20.4, we will describe how N and C isotopes were used to study the diets of both modern North American grizzly bears and extinct cave bears.

Stable isotopes can also be added to the environment to help trace the movements of elements. This approach is often used to trace the fate of nutrients in ecosystems.

Isotopic analysis of biological samples is relatively straightforward. For C and N, the samples are dried, ground, and burned in a closed furnace. The gases liberated by the combustion are then analyzed for isotopic composition using an instrument called a mass spectrometer. Many commercial laboratories specialize in the isotopic analysis of biological materials, owing in part to the demand for such analyses from ecologists and other environmental scientists.

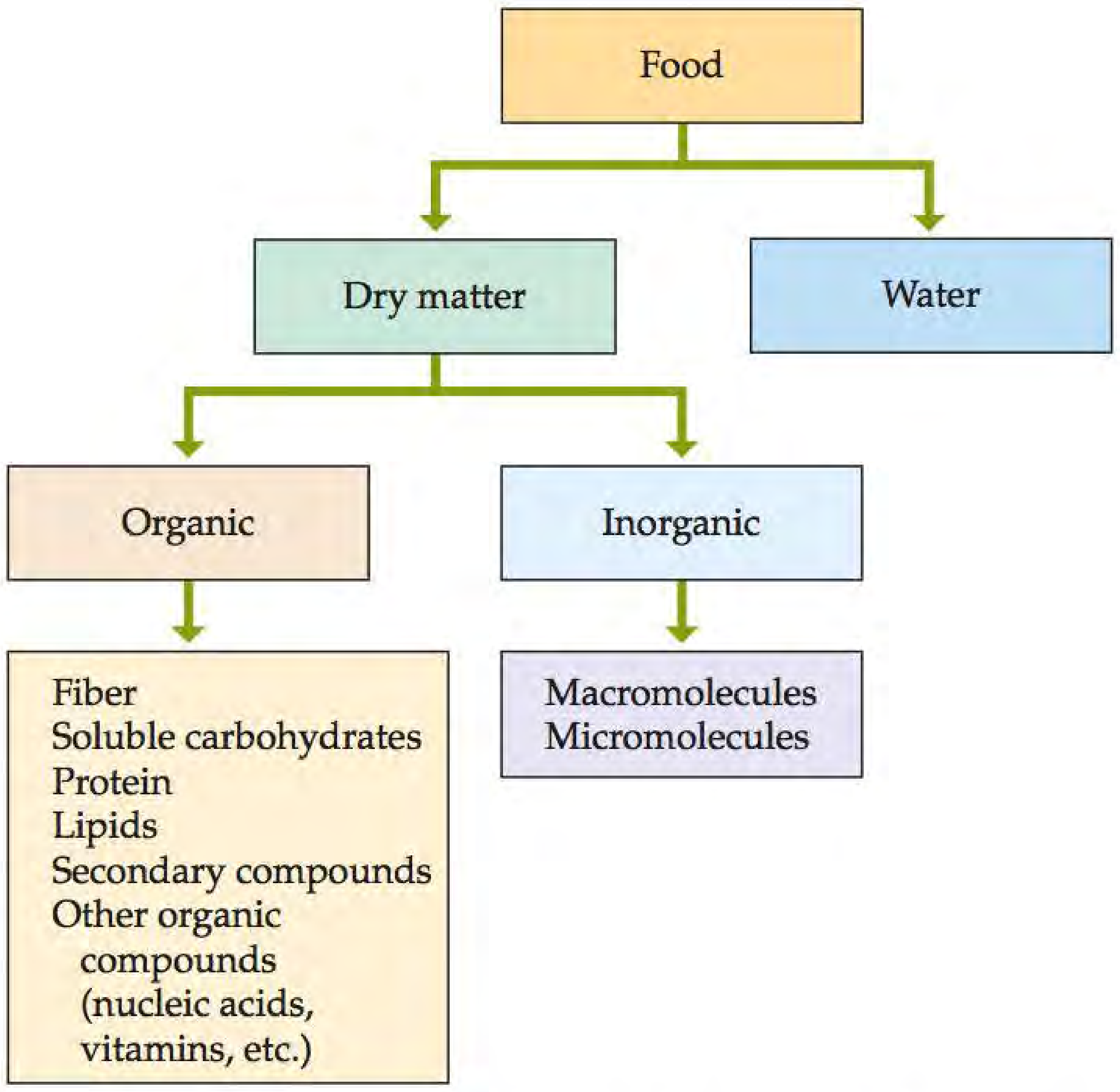


Figure 5.18 Categorical Breakdown of Food Chemistry Food chemistry can be complex, but these simple categories help ecologists understand how groups of chemicals influence the benefits of food for heterotrophs.

in the "dry matter" fraction (i.e., what is left when all the water is removed). *Fiber* includes compounds such as cellulose (the primary constituent of plant cell walls) and other structural components of organisms. It is generally a poor energy source because of its chemical structure and the inability of many heterotrophs to break it down chemically. Most of the energy in food is found in carbohydrates, proteins, and fats. Fats are richer in energy than carbohydrates per unit of mass, and carbohydrates provide more energy than the amino acids that make up proteins do. However, amino acids also provide nitrogen, a nutrient that is often in high demand. Secondary compounds (chemicals not used in growth or development) are generally not a good energy source for animals, and some secondary compounds may actually decrease energy intake by binding to digestive enzymes or by being directly toxic to the heterotrophs consuming them.

The differing concentrations of the compounds described in Figure 5.18 among food types are associated with the tissues, cell types, and organisms from which the food is derived. Animal tissues are generally more energy-rich than plant, fungal, or bacterial cells, which tend to have higher concentrations of fiber. As a result, *herbivores* (animals that eat plants) generally have to eat more food to get the same benefit that *carnivores* (animals that eat other animals) do. However, carnivores may expend substantially more energy finding food than herbivores do, as we will see in later chapters.

Heterotrophs obtain food using diverse strategies

Heterotrophs vary in size from archaea and bacteria (as small as 0.5 μm) to blue whales (up to 25 m long). The ratio of body size to food ingested varies widely, but it generally increases as body size increases. Bacteria may be bathed in their food, while food for larger heterotrophs is usually more diffuse and smaller relative to the consumer. Feeding methods and the complexity of food absorption are accordingly very diverse among heterotrophs.

Prokaryotic heterotrophs typically absorb food directly through their cell membranes. Archaea, bacteria, and fungi excrete enzymes into the environment to break down organic matter, acting in effect to digest their food outside their bodies. Heterotrophic bacteria have adapted to a wide variety of organic energy sources and produce a large number of enzymes capable of breaking down organic compounds. This capacity of microorganisms as a group to use diverse energy sources has been exploited in environmental waste management as an approach to cleaning up toxic chemical wastes, a process known as *bioremediation*. Spills of fuels, pesticides, sewage, and other toxins have been effectively contained by using microorganisms to break down these harmful compounds. Consumption of oil by marine bacteria is thought to have been an important contributor to cleaning up the oil spill in the Gulf of Mexico that resulted when the *Deepwater Horizon* oil drilling rig exploded in 2010, releasing about 4.9 million barrels (780 × 10^3 liters) of oil. Much of the oil was released directly to the deeper layers of the ocean from the wellhead, which flowed for 87 days unabated until it was finally capped (**Figure 5.19**). The oil spill posed a substantial hazard to marine life, and it was feared that its impact would be long-term, as the impacts of other oil spills had been. Some reports suggest that up to half the oil released in the *Deepwater Horizon* spill was consumed and respired by marine microorganisms (Du and Kessler 2012), although others suggest that the blooms of microorganisms observed after the spill resulted from consumption of natural gas that leaked from the well rather than the oil itself (Valentine et al. 2010). While the magnitude of consumption is still debated, it is clear that the environmental impact of the oil spill was lessened by the action of marine microorganisms that used the spilled oil as an energy source.

Multicellular heterotrophs usually must seek out food, or move it toward themselves in the case of some sessile marine animals. The evolution of mobility was probably associated with the need to seek out food sources, as well as with the need to avoid being eaten by other consumers. Continued morphological and behavioral adaptations for efficiently finding and capturing food in different environments led to additional diversification of form and function. Animals display tremendous diversity

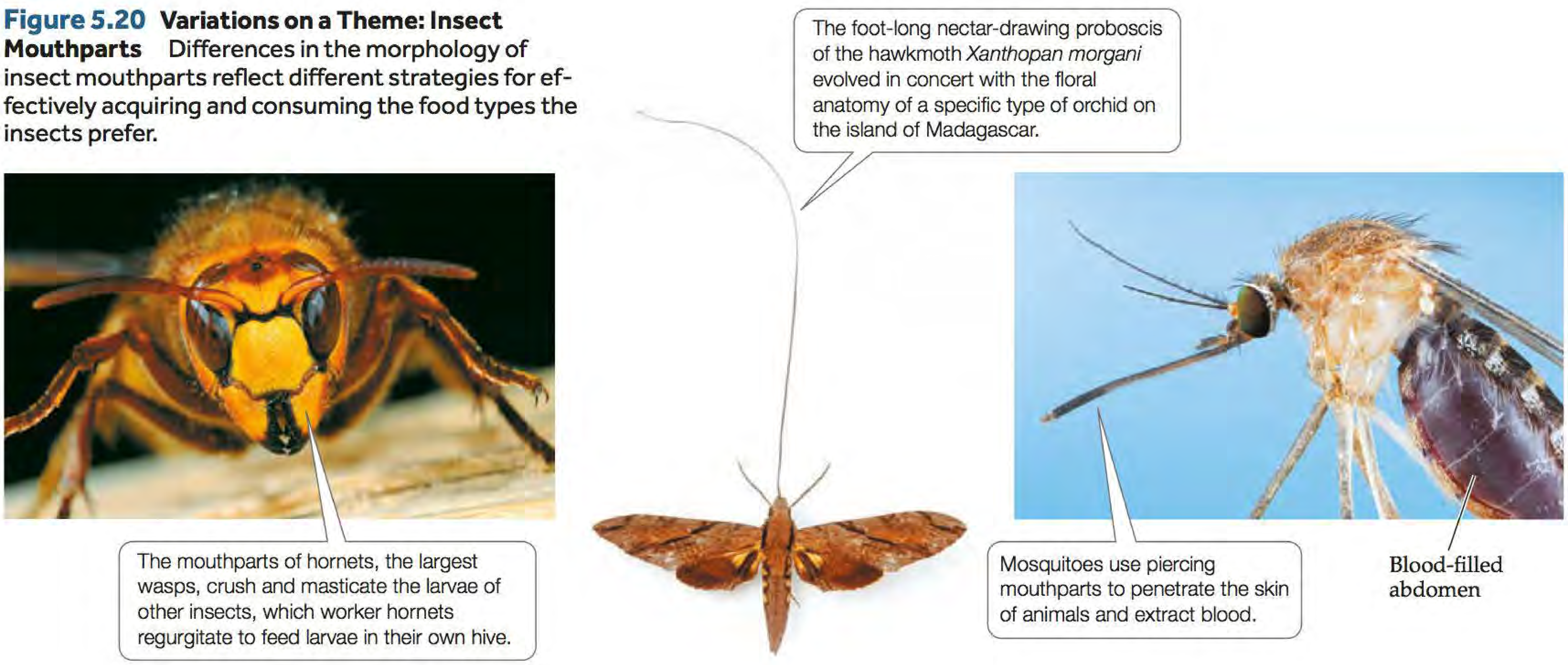
Figure 5.19 **An Environmental Disaster** Oil pours from the fractured wellhead of the *Deepwater Horizon* oil drilling rig at the seafloor 1,700 m (5,700 feet) below the surface. About 57,000 barrels (9.1 million liters) were released each day for more than 3 months. The impact of this disaster may have been somewhat lessened by the activities of marine microorganisms that were able to use the oil as an energy source.

in their specialized feeding adaptations, which reflect the diversity of the foods they consume. Here we present several examples that serve to demonstrate the morphological diversification of heterotrophs; we will take a closer look at behavioral adaptations for feeding in Concept 8.2.

MORPHOLOGICAL DIVERSITY OF INSECT MOUTHPARTS Insects display tremendous diversity in facial appearance, which reflects the diversity of their food sources, which include detritus, plants, and other animals. They may eat animal prey whole or suck out their body fluids. All insects have the same basic set of mouthparts, consisting of several paired appendages that are used to seize, handle, and consume their food. Morphological variation in these mouthparts reflects the feeding specializations that have evolved within different insect groups (**Figure 5.20**). Common houseflies have "sponging" mouthparts that release saliva onto their food, then soak up and ingest the partially digested solution. Female mosquitoes and aphids have piercing and sucking mouthparts for extracting fluids from their food sources—blood from animals and sap from plants. Biting flies have razor-sharp appendages that cut through skin to draw blood for drinking, similar to the cutting mouthparts of insects that consume leaves.

MORPHOLOGICAL ADAPTATION IN BIRD BILLS Like those of insects, the mouthparts of birds—that is, their bills—display morphological adaptations that reflect the multitude of ways they capture, manipulate, and consume their food (**Figure 5.21**). The morphology of a bird's bill is closely associated with the taxonomic group to which the bird belongs. In other words, the flat bills of ducks and the hooked bills of raptors vary little within those groups. However, subtle differences in bill morphology among closely related species reflect slight differences in food acquisition and handling. This variation reflects adaptations that help to optimize food acquisition and minimize competition among species (see Concept 14.2).

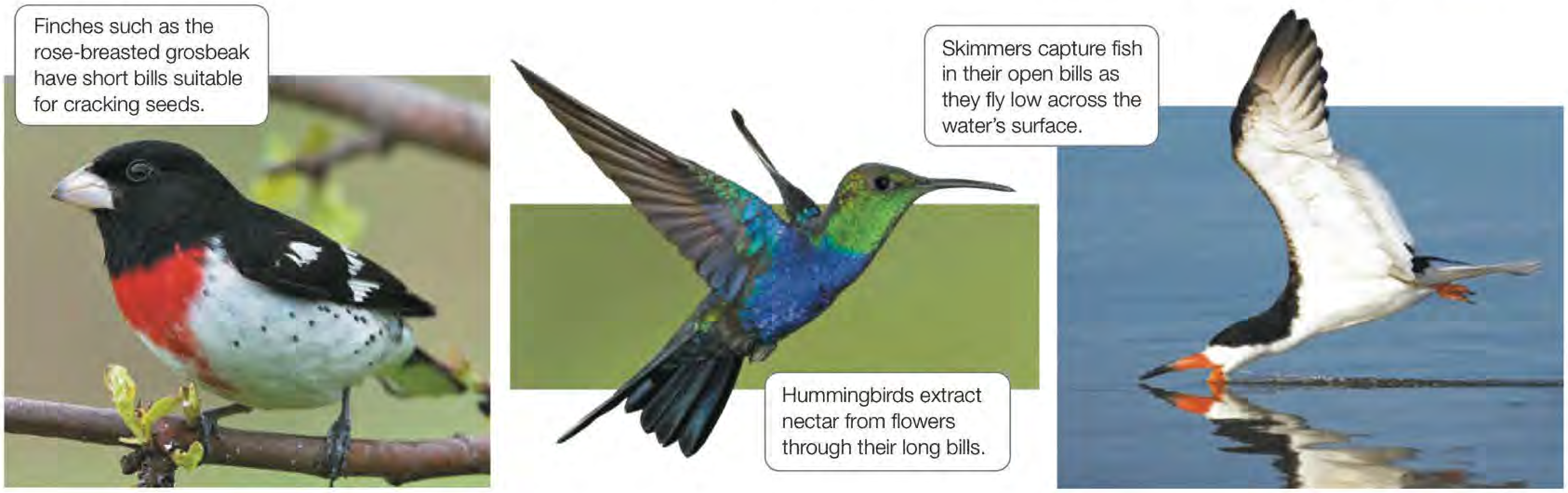
Figure 5.20 **Variations on a Theme: Insect Mouthparts** Differences in the morphology of insect mouthparts reflect different strategies for effectively acquiring and consuming the food types the insects prefer.



The foot-long nectar-drawing proboscis of the hawkmoth *Xanthopan morgani* evolved in concert with the floral anatomy of a specific type of orchid on the island of Madagascar.

The mouthparts of hornets, the largest wasps, crush and masticate the larvae of other insects, which worker hornets regurgitate to feed larvae in their own hive.

Mosquitoes use piercing mouthparts to penetrate the skin of animals and extract blood.



Finches such as the rose-breasted grosbeak have short bills suitable for cracking seeds.

Hummingbirds extract nectar from flowers through their long bills.

Skimmers capture fish in their open bills as they fly low across the water's surface.

Figure 5.21 Variations on a Theme: Bird Bills Bird bill morphology is associated with the feeding behavior of a species and enhances the acquisition of its preferred food resources.

Craig Benkman studied the relationship between differences in bill morphology among crossbills as they relate to differences in the conifer seeds they use as food (Benkman 1993, 2003). As their name indicates, crossbills have unique asymmetrical bills with crossing tips (**Figure 5.22A**). Crossbills are adept at using their bills to open the cones of coniferous trees and pull out seeds for consumption. Across their geographic range, crossbills have multiple conifer species available as potential food sources; however, the species that are most abundant vary across this range. Benkman wondered if there were differences in the bill morphologies of crossbills that were associated with the morphologies of the cones of their preferred conifer species.

Benkman tested this hypothesis experimentally using captive and wild birds from five incipient species (subspecies that are in the process of becoming species) of the red

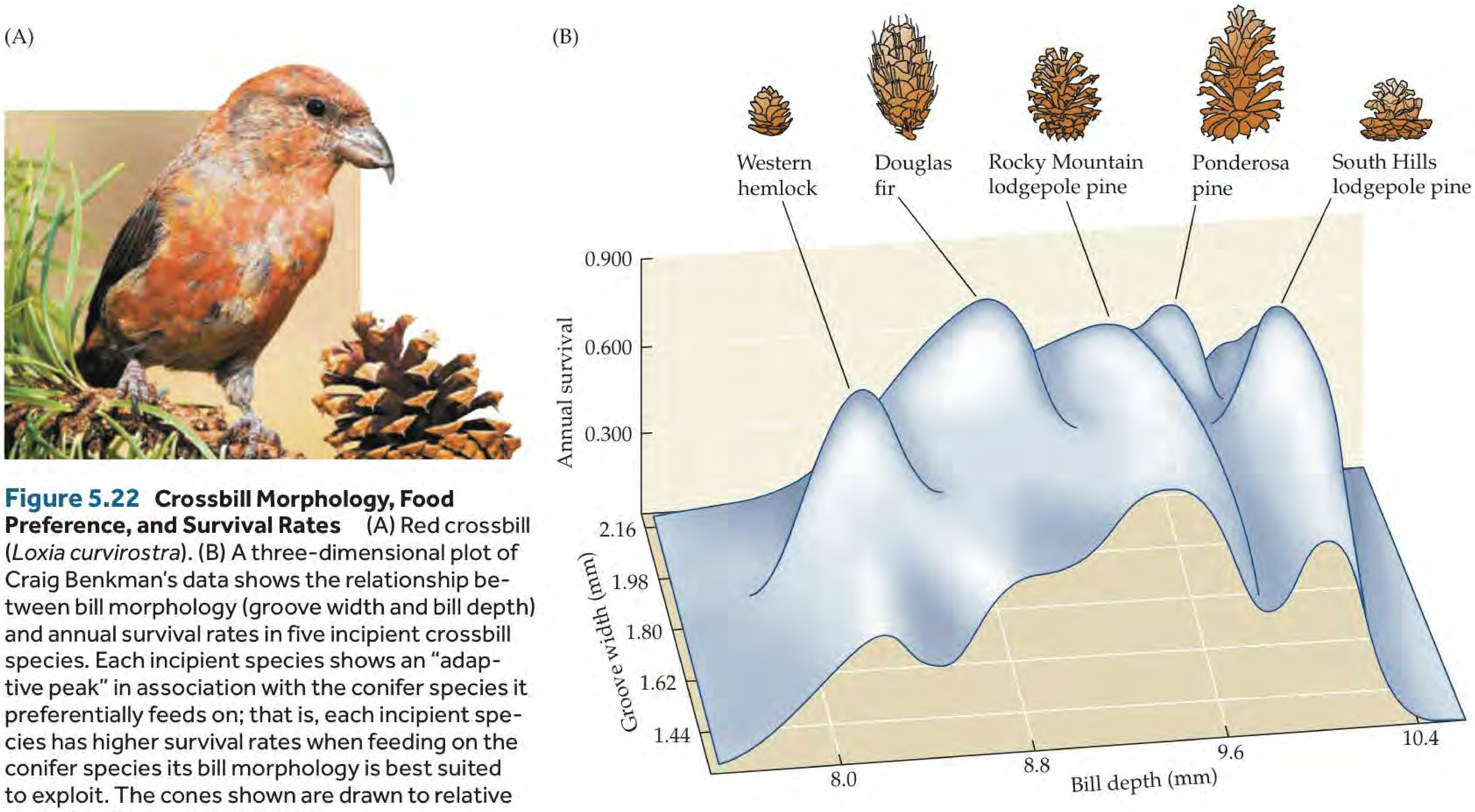


Figure 5.22 Crossbill Morphology, Food Preference, and Survival Rates (A) Red crossbill (*Loxia curvirostra*). (B) A three-dimensional plot of Craig Benkman's data shows the relationship between bill morphology (groove width and bill depth) and annual survival rates in five incipient crossbill species. Each incipient species shows an "adaptive peak" in association with the conifer species it preferentially feeds on; that is, each incipient species has higher survival rates when feeding on the conifer species its bill morphology is best suited to exploit. The cones shown are drawn to relative scale. (B after Benkman 2003.)

crossbill species complex (*Loxia curvirostra*). He showed in a series of studies that a bird's speed of seed extraction from a given conifer's cone was associated with its bill depth. In addition, Benkman demonstrated that the speed of seed husking (removing the outer cover) was associated with the width of the groove in the bill where the seed is held (Benkman 1993, 2003). Each incipient crossbill species extracted and husked the seeds of one conifer species more efficiently than the seeds of other conifers. The study showed an association between the bill depth of an incipient species and the depth at which the seeds are held in the cones of its preferred conifer species. Furthermore, Benkman found that the annual survival rate for each incipient crossbill species was related to its feeding efficiency, which varied according to the conifer species it was feeding on. When he put these results together, Benkman found a series of five "adaptive peaks," showing that bill morphology of each incipient species was associated with the conifer species on which it fed most efficiently and survived best (**Figure 5.22B**). Benkman (2003) concluded that red crossbills are currently undergoing evolutionary divergence (speciation; see Concept 6.4) as a result of selection associated with differences in available food resources across their range and the effects of those differences on bill morphology.

Heterotrophs vary in the complexity of their digestion and assimilation

As we have seen, food consumed by heterotrophs consists of a mix of complex compounds that must be chemically transformed into simpler compounds before they can be used as energy sources. Digestion breaks down proteins, carbohydrates, and fats into their component amino acids, simple sugars, and fatty acids. The evolution of digestion and assimilation are related to improving the efficiency of energy and nutrient extraction and to meeting the specific needs of physiological functions. Insect flight, for example, has a high energy demand, and some insects must maintain fat storage bodies to supply the energy required for initiation of flight. Humans require carbohydrates to fuel brain activity, which explains why low blood sugar can lead to poor cognitive ability. Thus, digestion and absorption of food are important steps in the energy acquisition and functioning of heterotrophs.

The evolution of feeding in heterotrophic protists and animals has led to increasing complexity in the ingestion, digestion, and absorption of food. Small protozoans such as amoebas and ciliates ingest food particles into their cells, where the food is digested in special organelles. With the advent of multicellular animals, specialized tissues for absorption, digestion, transport, and excretion evolved, and the efficiency of energy assimilation increased. Digestive systems evolved from simple chambers with a single input and output port, such as those in hydroid animals, to a tube with an input port (mouth) and an output port (anus). Further advancements included chambers specializing in specific digestive steps (e.g., stomachs) and absorption (e.g., intestines). Mechanisms evolved for breaking food down into smaller bits to increase the surface area exposed to digestion, including gizzards (which contain small rocks for grinding food) in earthworms and birds and molar teeth in mammals.

As you might guess from the discussion of food chemistry above, the diet of an animal can influence its digestive adaptations. For example, herbivores consume a food source—plants—that contains a large amount of fiber and small amounts of carbohydrates and proteins. To cope with this poor-quality diet, most herbivores have digestive tracts that are longer than those of carnivores, which increases food processing time and increases the surface area for absorbing energy (**Figure 5.23**). In order to further increase the exposure of food to the digestive tract, some herbivores, including many small vertebrate herbivores such as rabbits, reingest their feces (a strategy called *coprophagy*). Young animals may also ingest the feces of older animals. While this feeding strategy might seem disgusting to humans, it enhances the efficiency of digestion and absorption of poor-quality food, and it also helps to maintain a healthy colony of beneficial microorganisms in the animal's gut. Coprophagy generally does not seem to enhance the digestion of fiber in food, but instead is more

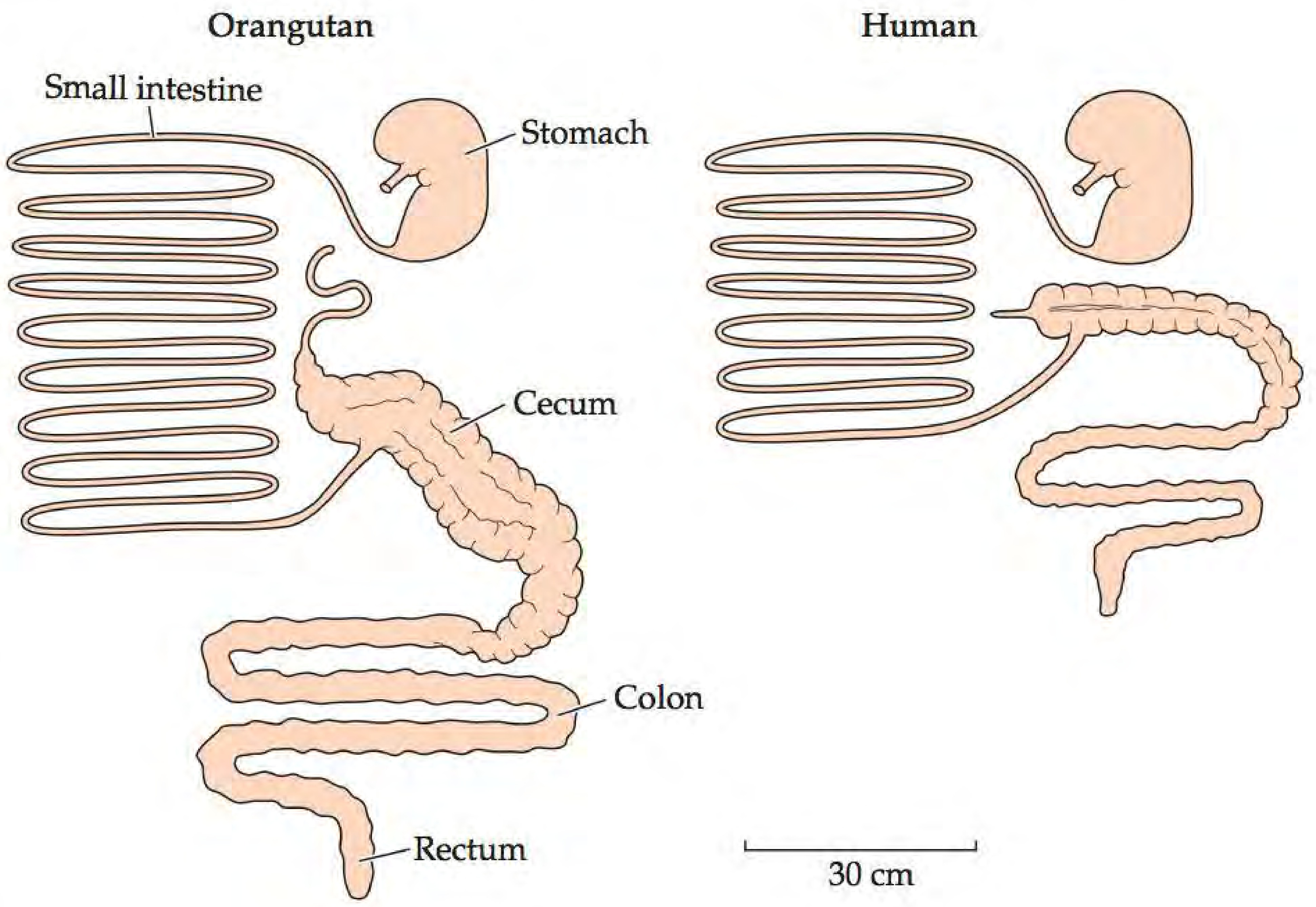


Figure 5.23 Herbivores Have Long Digestive Systems Compared with omnivorous humans, herbivorous primates such as the orangutan have longer digestive systems. The greater volume and absorptive area of herbivore digestive tracts serve to enhance energy absorption from poor-quality food. (After Wrong et al. 1981.)

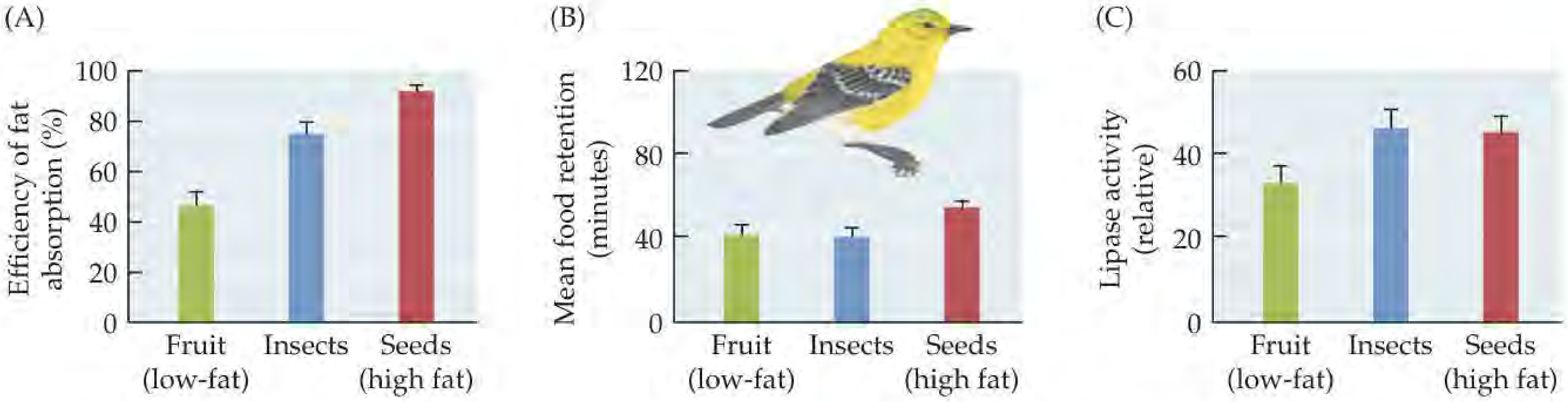


Figure 5.24 Adjustment of Digestion Efficiency with a Changing Diet Migrating warblers consume different diets in different parts of their ranges. To investigate the influence of fat content in the diet on their efficiency of fat absorption, researchers fed captive birds diets that were high (seed), medium (insect), or low (fruit) in fat, then measured the efficiency of fat absorption (the proportion of the fat in the diet taken up by the birds). The increase in the efficiency of fat absorption that accompanied a high-fat diet (A) was associated with longer food retention times (B) and greater production of a fat-degrading enzyme (lipase) by the pancreas (C). Error bars show one SE of the mean. (After Karasov and Martinez del Rio 2007.)

important for capturing vitamins and nutrients (Karasov and Martinez del Rio 2007).

Some herbivores have bacterial symbionts that greatly enhance the efficiency of digestion. Most animal digestive tracts are inhabited by archaea, bacteria, fungi, and even some protists, although the roles of many of these organisms in helping or hurting their hosts are unknown. For some animals, this relationship between the herbivore and its gut biota is clear: both benefit from the relationship. *Ruminants*, which include cattle and giraffes, have a specialized stomach compartment (the rumen) in which large populations of bacteria facilitate the chemical breakdown of cellulose into simple sugars. The rumen acts like a fermentation chamber, providing environmental conditions that favor the growth of these beneficial bacteria. Material from the rumen is eventually passed into another stomach chamber, which absorbs not only the compounds released from digested plant matter, but also the compounds released from the bacteria that accompany the mass of digested food. Ruminants also exhibit *rumination*, or cud chewing, which is the regurgitation of material from a forestomach for additional chewing. Rumination allows these animals to "eat on the run," consuming large amounts of plant material in a short time and thereby minimizing their exposure to predators that might consume them. They can then more thoroughly chew and digest their food at a later time when the threat of being eaten is lower.

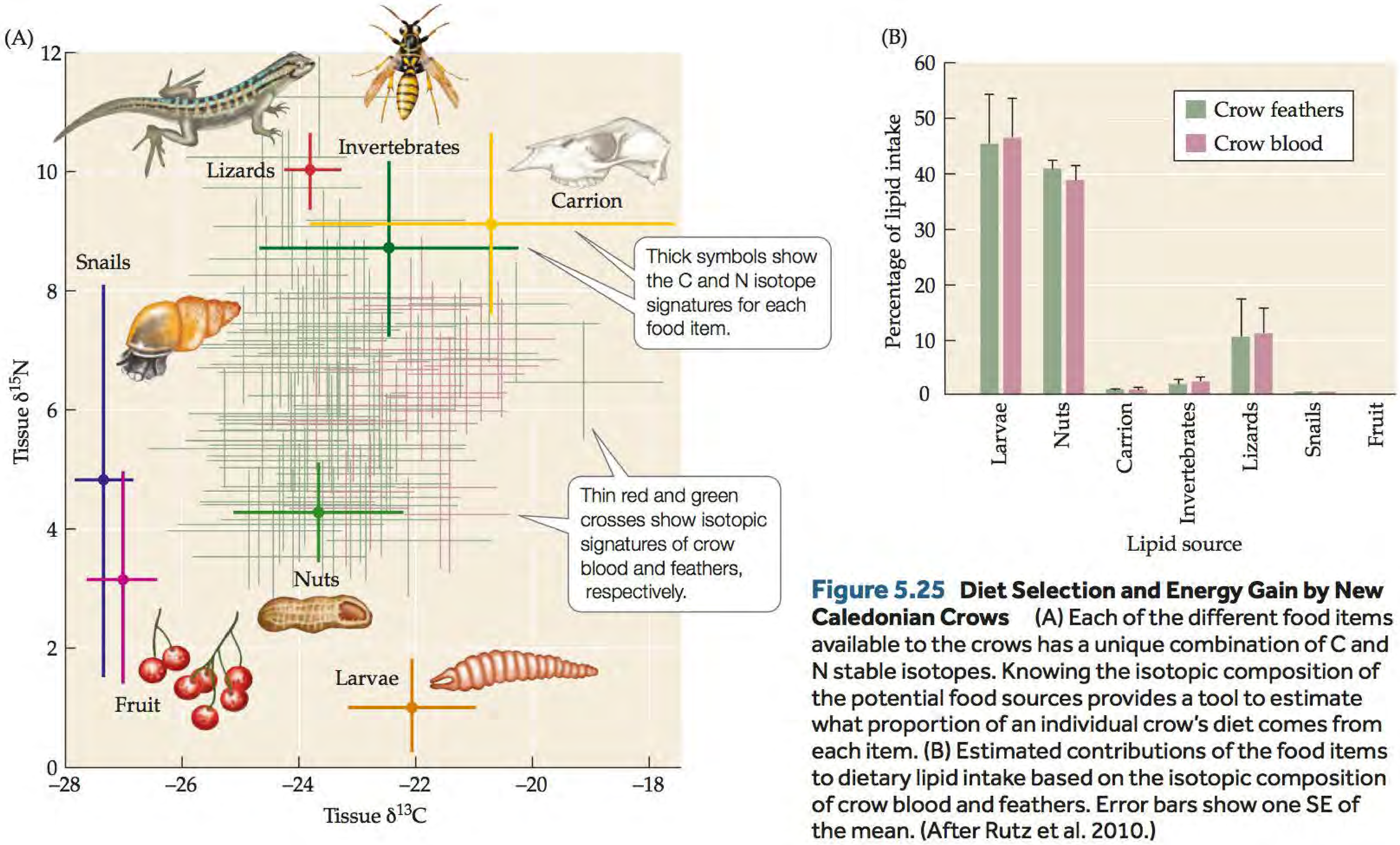
We've seen several examples of digestive adaptations to different food types. Can organisms acclimatize to eating different foods? The answer for some animals is yes. Organisms that consume a diverse diet of both plants and animals (*omnivores*) can adjust their digestive morphologies and produce different enzymes as needed to enhance digestion of their food. For example, warblers in the genus *Setophaga* make seasonal migrations that are associated with changes in their diet. The birds spend their breeding season (May–September) in forests of North America, eating mostly insects, and the rest of the year in Central America, consuming fruit and nectar. An experiment with captive warblers, including the pine warbler (*Setophaga pinus*), showed that their diets influenced the efficiency of fat assimilation. Compared with birds raised on diets of insects and fruit (which have a moderate and a low fat content, respectively), birds raised on seeds (which have a high fat content) showed the greatest ability to take up fats from their food due to longer food retention times in the gut and production of higher amounts of fat-degrading enzymes (**Figure 5.24**) (Karasov and Martinez del Rio 2007). This ability to acclimatize to different food sources allows omnivores such as warblers to select the best food source available at any given time. We'll discuss other aspects of diet flexibility and specialization in Concept 12.1.

A CASE STUDY REVISITED

Toolmaking Crows

We've seen that foraging animals often display behavioral as well as morphological and biochemical specializations that increase their efficiency in harvesting and digesting food. The specialized bill of crossbills is a morphological adaptation that improves their feeding efficiency. Warblers are able to adjust their digestive efficiencies to match their food source. Does tool use by crows enhance their ability to gain energy by allowing them to obtain food more efficiently or obtain food of higher quality?

New Caledonian crows are omnivores with a wide variety of food sources to select from, including vertebrate and invertebrate prey, plants, and dead animals (carrion). As we discussed earlier, the benefit a foraging animal gets from its food is determined by the effort it invests in finding and obtaining the food, the chemistry of the food, and the ability of the animal to digest and absorb it. There is a cost to tool use: collecting materials and fashioning the tools can be time-consuming, and young crows may not initially be adept at using them. Evaluating the benefit of



Thick symbols show the C and N isotope signatures for each food item.

Thin red and green crosses show isotopic signatures of crow blood and feathers, respectively.

Figure 5.25 Diet Selection and Energy Gain by New Caledonian Crows (A) Each of the different food items available to the crows has a unique combination of C and N stable isotopes. Knowing the isotopic composition of the potential food sources provides a tool to estimate what proportion of an individual crow's diet comes from each item. (B) Estimated contributions of the food items to dietary lipid intake based on the isotopic composition of crow blood and feathers. Error bars show one SE of the mean. (After Rutz et al. 2010.)

tool use to the crows requires knowledge of their energy requirements, the energetic benefits of their potential food sources, and the crows' actual diet.

The crows' shy nature and their tropical forest habitat make observational studies difficult. To evaluate the energetic benefit of toolmaking and tool use, Christian Rutz and colleagues (2010) used stable isotope measurements (see Ecological Toolkit 5.1) to evaluate what the birds were eating and then used measurements of the lipid content of their potential food sources to estimate the energetic benefits of each. They also estimated the energy demands of the crows. Initial observations suggested that the birds relied on two high-quality food items, both of which had a lipid content of about 40%: nuts from candlenut trees, which the crows crack open by dropping them onto rocks; and beetle larvae that these birds obtain by using tools. Stable isotope measurements of N and C in the crows' blood and feathers and in their potential food sources indicated that they used a variety of food resources (**Figure 5.25A**) but that over 80% of their lipid intake was coming from the nuts and larvae (**Figure 5.25B**). This result indicates that a large proportion of the crows' energetic demands are met using two behaviors: tool use and nut cracking.

To address whether tool-aided beetle larva extraction alone could meet the energetic demand of the crows, Rutz and his colleagues determined the minimum number of beetle larvae needed on a daily basis to sustain a crow of average weight. They found that only three larvae per day were needed, because of their high lipid content. Observations indicated that most adult crows can easily obtain three larvae per day; one competent adult crow was able to extract 15 larvae in 80 minutes. Tool use clearly provides a substantial benefit to the New Caledonian crows, giving them access to a high-quality food item that would otherwise not be available to them, or would at least require a very high investment of energy to obtain.

CONNECTIONS IN NATURE

Tool Use: Adaptation or Learned Behavior?

How widespread is tool use among birds and other nonprimate animals? Many anecdotes of toolmaking and other innovative foraging techniques have been reported, but few have been examined thoroughly. The orange-winged sittella (*Daphoenositta chrysoptera*) of Australia uses sticks to forage for insect larvae, much like the New Caledonian crows. Egyptian vultures (*Neophron percnopterus*) crack open ostrich eggs using rocks. There are additional reports of tool use by insects, mammals, and other bird species (Beck 1980). The multitude of reports involving a wide range of animal species thoroughly dispels the notion of human monopoly on tool use. But how do these tool-using skills

Figure 5.26 Untutored Tool Use in Captive Crows
A captive New Caledonian crow (*Corvus moneduloides*) uses a stick tool to retrieve food from artificial crevices in a laboratory setting, despite never having been exposed to tool use, either by humans or by other birds.

develop? Are these behaviors learned from other animals, or are they innate (i.e., determined genetically)? Several studies indicate that both learning and genetic inheritance can influence the development of tool use in animals.

As we learned above, tool use has a clear energetic benefit for New Caledonian crows, but does that benefit exert strong enough selection pressure to have resulted in a behavioral adaptation—are the birds inheriting the ability to use tools? To address this question, Ben Kenward and colleagues reared New Caledonian crows in captivity, without exposure to adult birds. Some of the birds received "tutoring" in toolmaking and tool use by human foster parents, while a control group did not (Kenward et al. 2005). To evaluate the birds' toolmaking abilities, the researchers placed supplemental food in tight crevices in the birds' aviaries, where it was not accessible to the birds without the assistance of tools. Twigs and leaves were also left in their aviaries. The captive crows developed the ability to make and use tools to retrieve the food in the crevices, whether they had been tutored or not (**Figure 5.26**). Kenward and colleagues concluded that the ability of New Caledonian crows to manufacture tools is at least partly inherited, rather than an acquired skill learned from adult birds in the wild. Very similar results were reported for experiments with captive woodpecker finches, birds endemic to the Galápagos archipelago that use twigs and cactus spines to forage for arthropods (Tebbich et al. 2001). Additional evidence that toolmaking is part of the genetic makeup of New Caledonian crows comes from an evaluation of their bill morphology, which has unique structural features consistent with tool manufacture and use as a selective force in its design (Matsui et al. 2016).

An additional twist to the crow toolmaking story is the apparent variation in tool styles among different crow populations on New Caledonia. In other words, there appears to be the potential for technological evolution in the styles of tools manufactured by crows. Gavin Hunt and Russell Gray conducted a survey of 21 sites on New Caledonia and examined 5,550 different cutting tools constructed by crows from *Pandanus* leaves (see Figure 5.2C) (Hunt and Gray 2003). They found three distinct widths of tools: wide, narrow, and stepped. Most of the tools found at a given site were very similar, and the geographic ranges of the tool types showed little overlap. There were no apparent correlations between where a tool type was found and local ecological factors such as forest structure or climate. Hunt and Gray suggested that the three tool designs were derived from a single original tool (of the wide type) subjected to additional modifications, including additional stripping of leaf material. Their study suggests ongoing innovation in toolmaking by the New Caledonian crows. This crow engineering challenges our traditional view of technological advancement in nonhuman animals.

Learned behavior is also important for toolmaking in some species. A notable example comes from studies of bottlenose dolphins in Shark Bay, Australia. Researchers observed that some dolphins swim with sponges plucked from the ocean floor on their noses (technically, their rostra) (**Figure 5.27**). The sponges appear to protect the sensitive rostra from sharp objects and stinging animals such as stonefish as the dolphins probe the seafloor

Figure 5.27 Dolphin Nose Gear in Shark Bay, Australia
A bottlenose dolphin wears a sponge to protect its rostrum while foraging on the seafloor.

for fish. The group of dolphins displaying this innovation is part of a larger group under study. The researchers' knowledge of the genetics and family structure of these dolphins allowed them to address the question of whether this unique behavior is learned or inherited. Michael Krützen and colleagues found that the majority of "sponging" dolphins were female. They reasoned that a single sex-linked gene (the kind of genetic basis one might expect for a trait occurring in only one sex) was a highly unlikely cause for a complex trait such as sponging. A comparison of the genetic fingerprints of individuals that sponged with those of nonsponging dolphins indicated that most of the sponging occurred within a single family line (Krützen et al. 2005). The combination of these results led Krützen and colleagues to conclude that sponging was a learned behavior passed from mother to daughter. This finding supports the idea of a cultural phenomenon in animals that influences the efficiency of their feeding behavior and challenges the notion that cultural learning is unique to humans.

Summary

CONCEPT 5.1 Organisms obtain energy from sunlight, from inorganic chemical compounds, or through the consumption of organic compounds.

- Autotrophs convert energy from sunlight (by photosynthesis) or inorganic chemicals (by chemosynthesis) into energy stored in the carbon–carbon bonds of carbohydrates.
- Heterotrophs acquire energy by consuming organic compounds from other organisms, living or dead.

CONCEPT 5.2 Radiant and chemical energy captured by autotrophs is converted into stored energy in carbon–carbon bonds.

- During chemosynthesis, bacteria and archaea oxidize inorganic substrates to obtain energy, which they use to fix carbon and synthesize sugars.
- Photosynthesis has two main steps: the absorption of sunlight by pigments to produce energy in the form of ATP and NADPH (the light-driven reactions), and the use of that energy in the Calvin cycle to fix CO_2 and synthesize carbohydrates (the carbon reactions).
- Photosynthetic responses to variation in light levels, water availability, and nutrient availability include both short-term acclimatization and long-term adaptation.

CONCEPT 5.3 Environmental constraints have resulted in the evolution of biochemical pathways that improve the efficiency of photosynthesis.

- Photorespiration operates in opposition to photosynthesis, lowering the rate of energy gain, particularly at high temperatures and low atmospheric CO_2 concentrations.
- The C_4 photosynthetic pathway concentrates CO_2 at the site of the Calvin cycle, minimizing photorespiration.
- CAM plants reduce transpirational water loss by opening their stomates at night to take up CO_2 and releasing it to the Calvin cycle during the day, when the stomates are closed.

CONCEPT 5.4 Heterotrophs have adaptations for acquiring and assimilating energy efficiently from a variety of organic sources.

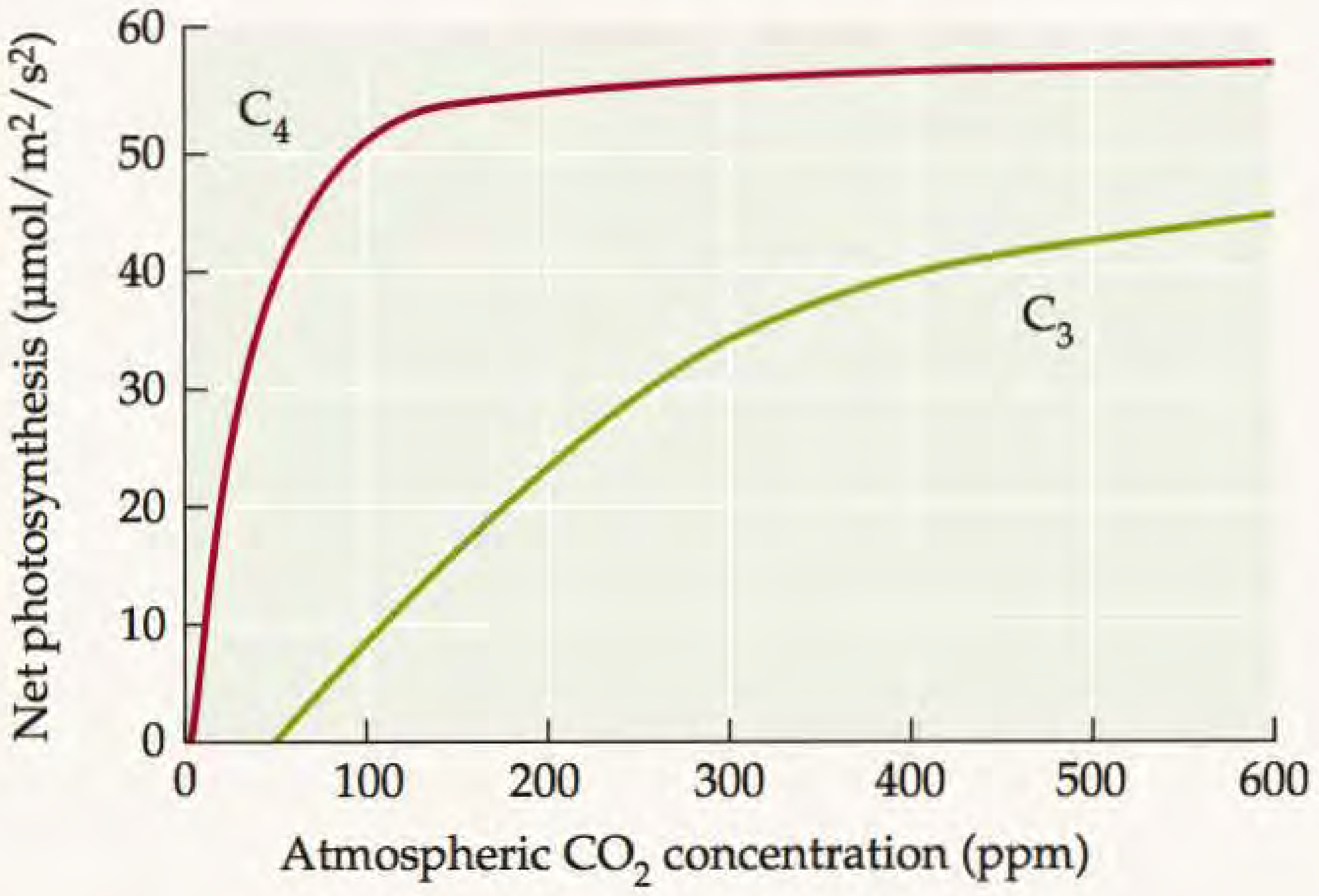
- Variations in the chemistry and availability of food determine how much energy heterotrophs gain from different food sources.
- Heterotrophs display tremendous diversity in behavioral, morphological, and physiological adaptations that enhance their efficiency of energy acquisition and assimilation.

Review Questions

1. Define autotrophy and heterotrophy, and provide a few examples of each that illustrate the diversity of the ways in which organisms obtain energy.
2. How does the CAM photosynthetic pathway influence water loss from plants?
3. What are the trade-offs associated with heterotrophic consumption of live animals versus dead plant material?

Hone Your Problem-Solving Skills

Our earlier comparison of the C_3 and C_4 photosynthetic pathways emphasized the benefit of the C_4 pathway through its capacity to minimize photorespiration by increasing the concentration of CO_2 inside the leaf. With the advent of elevated atmospheric CO_2 concentrations over the past century, ecologists have speculated whether C_3 plants might benefit more than C_4 plants from possible CO_2 fertilization. Such speculation is based on laboratory measurements and modeling of plant responses to variation in CO_2 concentrations. An example is such as shown in the figure below (After Lambers et al. 2008).



1. Based on the modeled response in the figure, what are the absolute and relative (as a percent) increases in photosynthesis for C_3 and C_4 plants from preindustrial levels of CO_2 (280 ppm) to the current level of CO_2 (400 ppm)? What are the possible consequences of any differences in the responses of C_3 and C_4 plants to elevated CO_2 in plant communities where they co-occur and compete for limited resources?
2. A review of 62 studies examining the responses of C_3 and C_4 grasses to elevated CO_2 found that on average photosynthesis increased by 33% and 25% in these groups, respectively (Wand et al. 1999). How does this compare with your estimate from Question 1? What might account for any discrepancies? Possible contributions may be related to the influence of CO_2 on lowering stomatal opening and the demand for nitrogen to make enzymes.

ON THE COMPANION WEBSITE

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The website includes companions to all of the Analyzing Data exercises, Online Quizzes, Flashcards, Suggested Readings, and more. In addition, the following resources are available for this chapter:

Hands-On Problem Solving

5.1 Some Like It Hot: Comparison of C_3 and C_4 Pathways

Web Extensions

5.1 How Do Plants Cope with Too Much Light?

Online Climate Change Connection

5.1 Recently Discovered Pigment May Lead to More Efficient Solar Energy Systems

Unit 2

Evolutionary Ecology

6 Evolution and Ecology

KEY CONCEPTS

CONCEPT 6.1 Evolution can be viewed as genetic change over time or as a process of descent with modification.

CONCEPT 6.2 Natural selection, genetic drift, and gene flow can cause allele frequencies in a population to change over time.

CONCEPT 6.3 Natural selection is the only evolutionary mechanism that consistently causes adaptive evolution.

CONCEPT 6.4 Long-term patterns of evolution are shaped by large-scale processes such as speciation, mass extinction, and adaptive radiation.

CONCEPT 6.5 Ecological interactions and evolution exert a profound influence on one another.

Trophy Hunting and Inadvertent Evolution: A Case Study

Bighorn sheep (*Ovis canadensis*) are magnificent animals, beautifully suited for life in the rugged mountains in which they are found. Despite their substantial size (males can weigh up to 127 kg, or 280 pounds), these sheep can balance on narrow ledges and can leap 6 m (20 feet) from one ledge to another. Bighorn sheep are also noted for the male's large curl of horns, which are used in combat over females (**Figure 6.1**). Rams run at speeds of up to 20 miles per hour and crash their heads into each other, battling over the right to mate with a female.

Ram horns have been collected as trophies for many centuries without drastically affecting sheep populations. Over the last 200 years, however, human actions such as habitat encroachment, hunting, and the introduction of domesticated cattle have reduced populations of bighorn sheep by 90%. As a result, the hunting of bighorn sheep has been restricted throughout North America. These restrictions make a world-class trophy ram (one with a large, full curl of horns) extremely valuable: permits to shoot one of these rams, which are sold at auction, can cost over $100,000.

Although funds raised by the auction of hunting permits are used to preserve bighorn sheep habitat, scientists have expressed concern that trophy hunting is having negative effects on today's small populations of bighorn sheep. Trophy hunting removes the largest and strongest males: in a population from which about 10% of the males were removed by hunting each year, both the average size of males and the average size of their horns decreased over a 30-year period (**Figure 6.2**). Large and strong males tend to sire more offspring than other males, so killing the largest and strongest males can make it harder for small populations to recover in size.

Hunting, fishing, and other forms of harvest have affected a wide range of other species, including fishes, invertebrates, and plants (Darimont et al. 2009). For example, by targeting older and larger fish, commercial fishing for cod has led to a reduction in the age and size at which these fish become sexually mature. To see why this happens, first note that cod that mature at a younger age and smaller size are more likely to reproduce before they are caught than are fish that mature when they are older and larger. As a result, the genes of fish that mature at a younger age and smaller size are more likely to be passed on to the next generation than are the genes of other fish—hence, we would predict that over time, more and more fish will have genes that encode sexual maturity at a younger age and smaller size. Indeed, in experimental populations of guppies in which small or large individuals

Figure 6.1 Fighting over the Right to Mate Large male bighorn sheep with a full curl of horns—the same males prized by trophy hunters—are the most successful in contests over the right to mate with females.

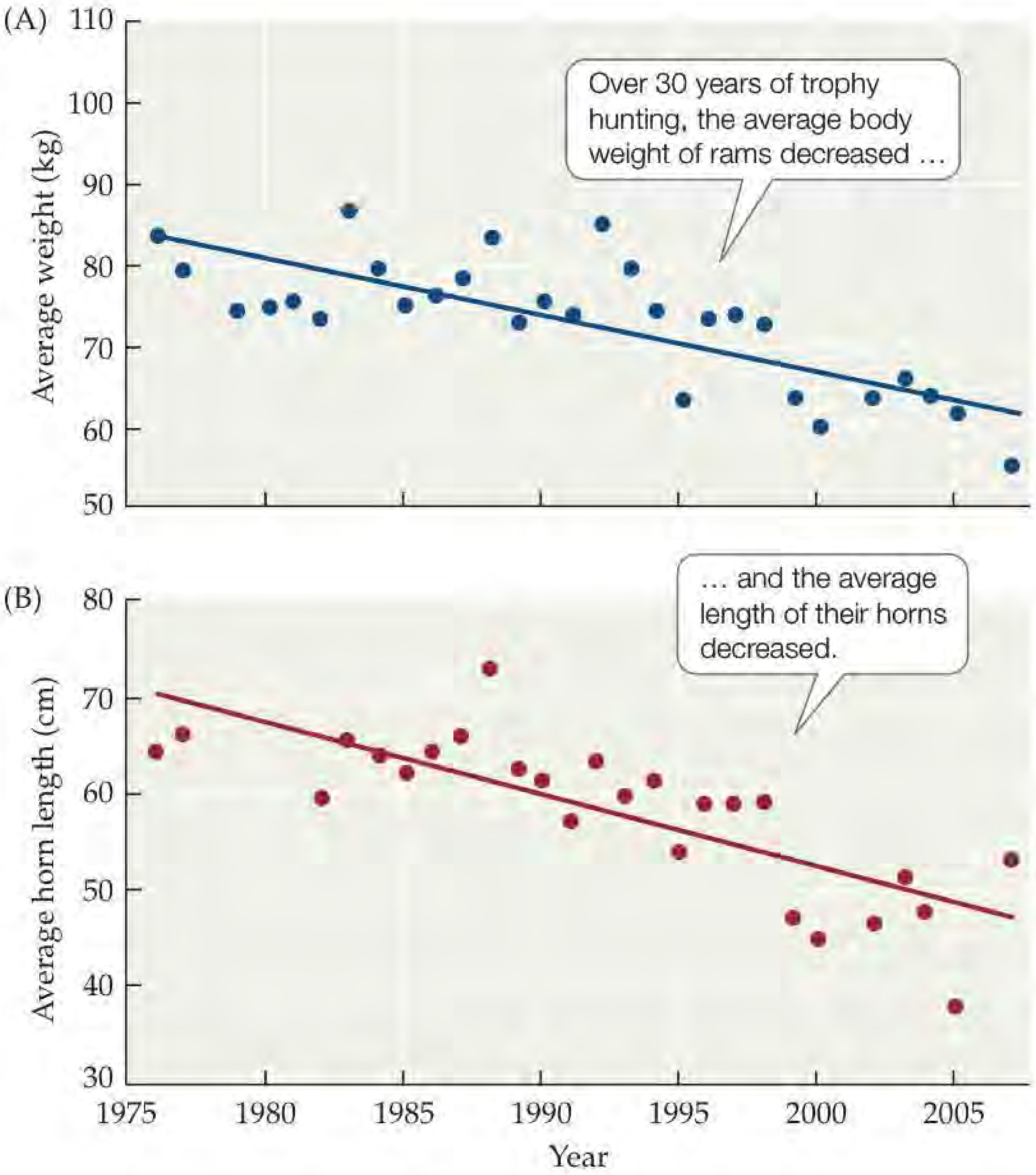


Figure 6.2 **Trophy Hunting Decreases Ram Body and Horn Size** Coltman and colleagues tracked the body weights (A) and horn lengths (B) of rams in a bighorn sheep population on Ram Mountain (Alberta, Canada) that was subjected to trophy hunting over a 30-year period. The changes shown here occurred across multiple generations of sheep and thus indicate a change in the average characteristics of the sheep born from one generation to the next. (After Coltman et al. 2003.)

were selectively removed for harvest, van Wijk et al. (2013) documented such genetic changes in genes known to affect body size. Similarly, poaching for ivory appears to have resulted in genetic changes that have caused the proportion of female African elephants in a South African park that lack tusks to increase from 62% to 90% over a 20-year period.

The unintended effects of human harvesting on bighorn sheep, cod, and elephants illustrate how populations can change, or *evolve*, over time. What biological mechanisms cause these evolutionary changes? Do human actions other than harvesting produce evolutionary change?

Introduction

As news reports often emphasize, humans have a large effect on the environment. We change the global climate, pollute the water and air, convert large tracts of natural habitat into farmland and urban areas, drain wetlands, and reduce the population sizes of species we hunt for food (e.g., fishes) or use as resources (e.g., trees). Although we have taken steps to limit some of the damage we cause to biological communities, human actions have a pervasive consequence that we have barely begun to recognize, much less address: we cause evolutionary change.

In this chapter, we'll examine what evolution is, and we'll see how it affects ecological interactions and is affected by them. At the close of the chapter, we'll focus specifically on how humans cause evolutionary change. Our goal in this chapter is not to provide a comprehensive survey of evolutionary biology—for that, see the textbooks on evolution listed in the Suggested Readings on the book's website. Instead, our aim is to show that ecology and evolution are interconnected, a theme to which we will return in later chapters of this book. We'll begin by considering two ways in which evolution can be defined.

CONCEPT 6.1

Evolution can be viewed as genetic change over time or as a process of descent with modification.

What Is Evolution?

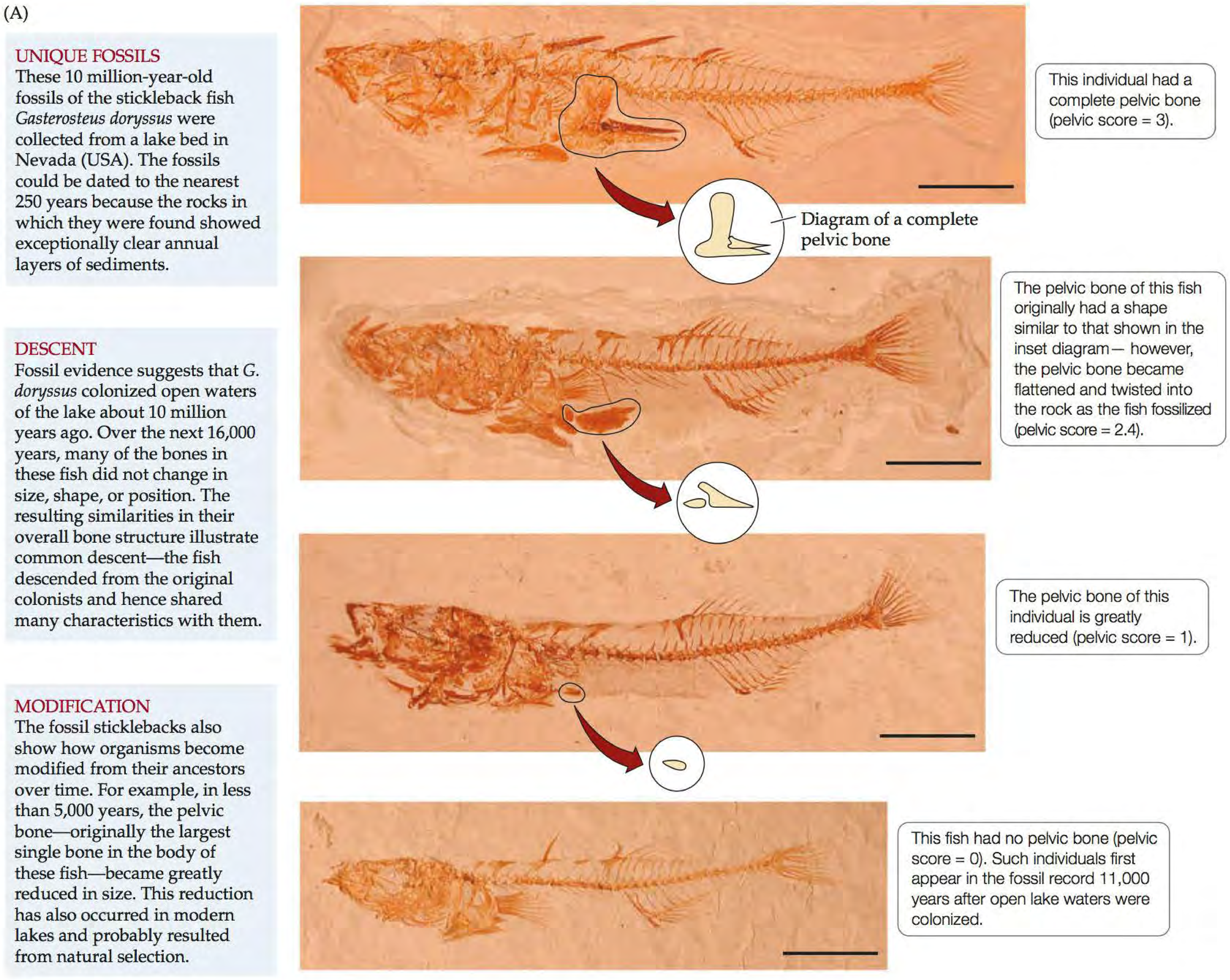
In the most general sense, biological evolution is change in organisms over time. Evolution includes the relatively small fluctuations that occur continually within populations, as when the genetic makeup of a population changes from one year to the next. But evolution can also refer to the larger changes that occur as species gradually become increasingly different from their ancestors. Let's explore these two ways of looking at evolution in more detail, focusing first on genetic changes (*allele frequency change*) and then on how organisms accumulate differences from their ancestors (*descent with modification*).

Evolution is allele frequency change

Figure 6.2B shows that the average horn size of male bighorn sheep has decreased over time, but it does not reveal the cause of that decline. A clue to the cause comes from an additional observation (Coltman et al. 2003): horn size is a *heritable* trait. This means that rams with large horns tend to have offspring that have large horns and that rams with small horns tend to have offspring that have small horns. Because trophy hunting selectively eliminates rams with large horns, it favors rams whose genetic characteristics lead to the production of small horns. Hence, it seems likely that trophy hunting is causing the genetic characteristics of the bighorn sheep population to change, or evolve, over time—a conclusion supported in a recent analysis of data from a bighorn sheep population subjected to intense hunting for 23 years (Pigeon et al. 2016).

As suggested by the trophy-hunting example, biologists often define evolution in terms of genetic change. To make such a definition more precise (and to introduce terms that will be used throughout this chapter), let's review some principles from introductory biology:

- Genes are composed of DNA, and they specify how to build (encode) proteins.



UNIQUE FOSSILS
These 10 million-year-old fossils of the stickleback fish *Gasterosteus doryssus* were collected from a lake bed in Nevada (USA). The fossils could be dated to the nearest 250 years because the rocks in which they were found showed exceptionally clear annual layers of sediments.

DESCENT
Fossil evidence suggests that *G. doryssus* colonized open waters of the lake about 10 million years ago. Over the next 16,000 years, many of the bones in these fish did not change in size, shape, or position. The resulting similarities in their overall bone structure illustrate common descent—the fish descended from the original colonists and hence shared many characteristics with them.

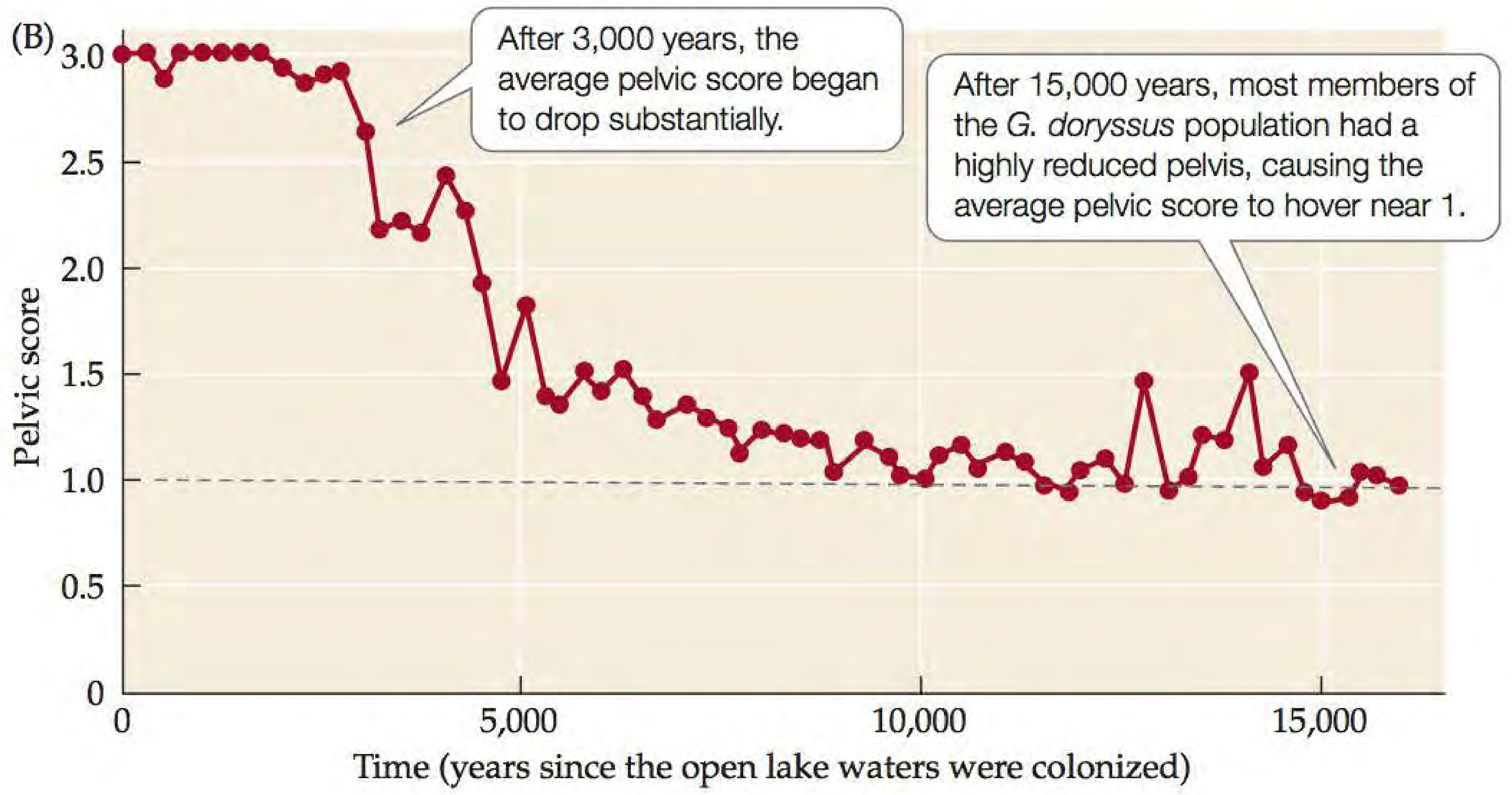
MODIFICATION
The fossil sticklebacks also show how organisms become modified from their ancestors over time. For example, in less than 5,000 years, the pelvic bone—originally the largest single bone in the body of these fish—became greatly reduced in size. This reduction has also occurred in modern lakes and probably resulted from natural selection.

This individual had a complete pelvic bone (pelvic score = 3).

The pelvic bone of this fish originally had a shape similar to that shown in the inset diagram— however, the pelvic bone became flattened and twisted into the rock as the fish fossilized (pelvic score = 2.4).

The pelvic bone of this individual is greatly reduced (pelvic score = 1).

This fish had no pelvic bone (pelvic score = 0). Such individuals first appear in the fossil record 11,000 years after open lake waters were colonized.



After 3,000 years, the average pelvic score began to drop substantially.

After 15,000 years, most members of the *G. doryssus* population had a highly reduced pelvis, causing the average pelvic score to hover near 1.

Figure 6.3 Descent with Modification Michael Bell and colleagues have analyzed thousands of 10 million-year-old fossils of the stickleback fish *Gasterosteus doryssus*. Their specimens are unique in that the lake bed in which they were found is so finely layered that the ages of the fossils can be determined to the nearest 250-year interval. (A) Representative *G. doryssus* fossils, showing how the pelvic bone became reduced over time; the scale bar for each fossil is 1 cm. (B) The average pelvic score at different times. Fossil pelvic bones were scored by size according to a scale that ranged from 3 (complete bone) to 0 (no bone). (After Bell et al. 2006; images courtesy of M. P. Travis and P. J. Park.)

- A given gene can have two or more forms (known as **alleles**) that result in the production of different versions of the protein that the gene encodes.
- We can designate the **genotype** (genetic makeup) of an individual with letters that represent the individual's two copies of each gene (one inherited from its mother, the other from its father). For example, if a gene has two alleles, designated *A* and *a*, the individual could be of genotype *AA*, *Aa*, or *aa*.

With these principles as background, we can define **evolution** as change over time in the *frequencies* (proportions) of different alleles in a population. To illustrate how this definition is applied, consider a population of 1,000 individuals and a gene with two alleles (*A* and *a*). Suppose there are 360 individuals of genotype *AA*, 480 of genotype *Aa*, and 160 of genotype *aa*. The frequency of the *a* allele in this population is 0.4, or 40%;[1] hence, since there are only two alleles in the population (*A* and *a*), the frequency of the *A* allele must be 1 – 0.4 = 0.6, or 60%. If the frequency of the *a* allele were to change over time, say, from 40% to 71%, then the population would have evolved at that gene. (In scientific studies, researchers often use an approach based on the *Hardy–Weinberg equation* to test whether a population is evolving at one or more genes; we describe this approach in **Web Extension 6.1**.)

Evolution is descent with modification

In many parts of this book, when we refer to evolution, we will be referring to allele frequency change over time. But evolution can also be defined more broadly as *descent with modification*. At the heart of this definition is the observation that populations accumulate differences over time, and hence, when a new species forms, it differs from its ancestors. However, although a new species differs from its ancestors in some ways, it also resembles its ancestors and continues to share many characteristics with them. Hence, when evolution occurs, both *descent* (shared ancestry, resulting in shared characteristics) and *modification* (the accumulation of differences) can be observed, as seen in the fossil fish in **Figure 6.3**.

Charles Darwin (1859) used the phrase "descent with modification" to summarize the evolutionary process in his book *The Origin of Species*. Darwin proposed that populations accumulate differences over time primarily by **natural selection**, the process by which individuals with certain heritable characteristics survive and reproduce more successfully than other individuals because of those characteristics. We've already seen several examples of selection at work in this chapter's Case Study. In bighorn sheep populations, trophy hunting has selected for rams with small horns, while in the cod fishery, harvesting practices have selected for individuals that mature at a younger age and a smaller size.

How can natural selection explain the accumulation of differences between populations? Darwin argued that if two populations experience different environmental conditions, individuals with one set of characteristics may be favored by natural selection in one population, while individuals with a different set of characteristics may be favored in the other population (**Figure 6.4**). By favoring individuals with different heritable characteristics in different populations, natural selection can cause populations to diverge genetically from one another over time; that is, each population will accumulate more and more genetic differences. Thus, natural selection can be responsible for the *modification* part of "descent with modification."

Populations evolve, individuals do not

Natural selection acts as a sorting process, favoring individuals with some heritable traits (e.g., those with small horns) over others (e.g., those with large horns). Individuals with the favored traits tend to leave more offspring than do individuals with other traits. As a result, from one generation to the next, a greater proportion of the individuals in the population will have the traits favored by natural selection. This process can cause the allele frequencies

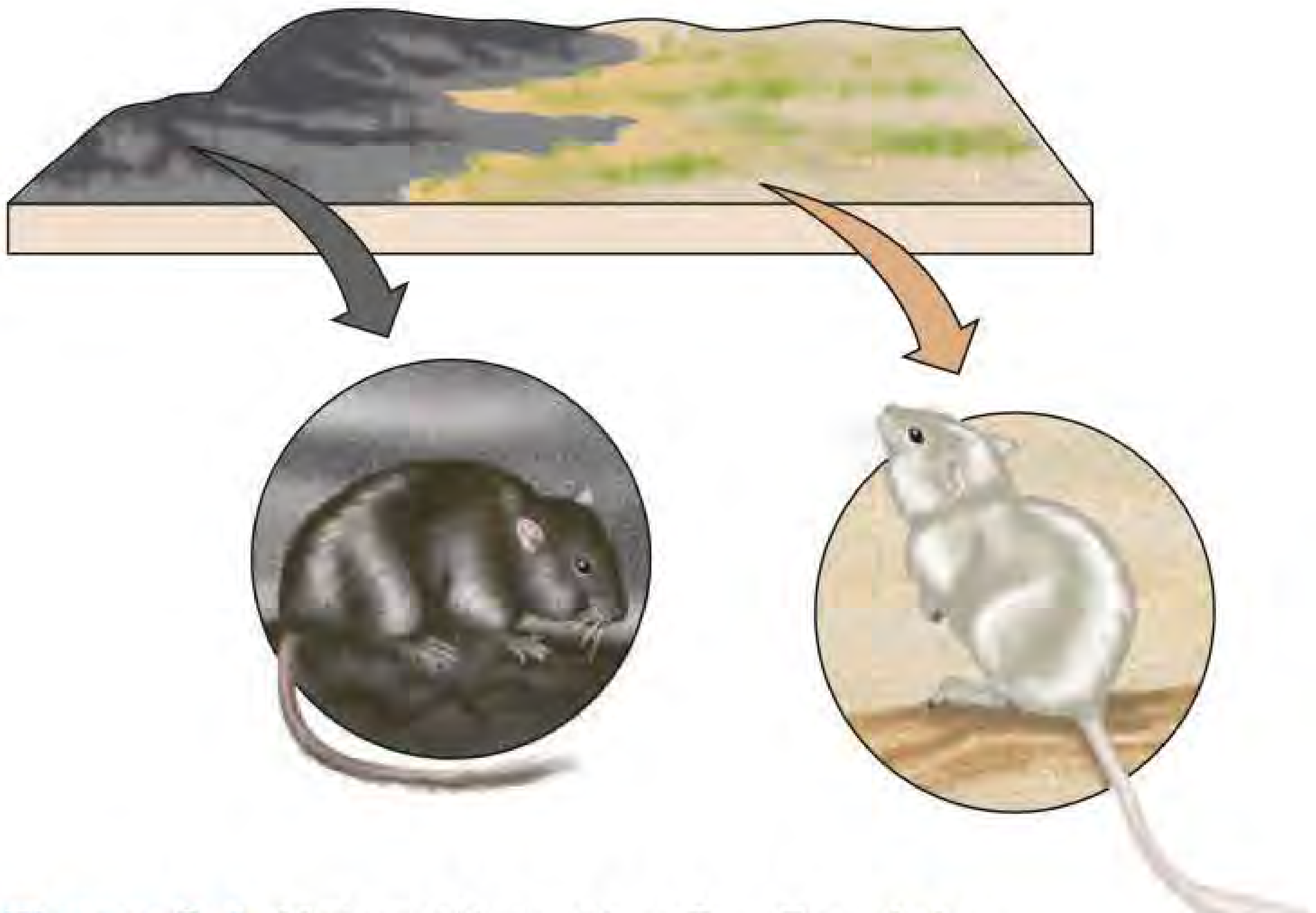


Figure 6.4 Natural Selection Can Result in Differences between Populations Populations of rock pocket mice (*Chaetodipus intermedius*) that live on dark lava formations in Arizona and New Mexico have dark coats, while nearby populations that live on light-colored rocks have light coats. In each population, natural selection has favored individuals whose coat colors match their surroundings, making them less visible to predators.

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[1] Each of the 1,000 individuals in the population has two alleles, giving a total of 2,000 alleles in the population. Each of the 360 individuals of genotype *AA* has zero *a* alleles, each of the 480 individuals of genotype *Aa* has one *a* allele, and each of the 160 individuals of genotype *aa* has two *a* alleles. Thus, the frequency of the *a* allele is $(0 \times 360 + 1 \times 480 + 2 \times 160)/2{,}000 = 0.4$. The frequency of the *a* allele can also be calculated using genotype frequencies, in which case we have $[(0 \times 0.36) + (1 \times 0.48) + (2 \times 0.16)]/2 = 0.4$, where $360/1{,}000 = 0.36$ is the frequency of genotype *AA*, 0.48 is the frequency of genotype *Aa*, and 0.16 is the frequency of genotype *aa*.

of the population to change over time, thereby causing the population to evolve. But the *individuals* in the population do not evolve—either they have the traits favored by selection or they don't.

CONCEPT 6.2
Natural selection, genetic drift, and gene flow can cause allele frequencies in a population to change over time.

Mechanisms of Evolution

Although natural selection is often the cause of evolutionary change, it is not the only one. In this section, we'll examine four key processes that influence evolution: mutation, natural selection, genetic drift, and gene flow. In broad overview, mutation is the source of the new alleles on which all of evolution depends, while natural selection, genetic drift, and gene flow are the main mechanisms that cause allele frequencies to change over time.

Mutation generates the raw material for evolution

Individuals in populations differ from one another in their observable characteristics, or **phenotype** (**Figure 6.5**). Many aspects of an organism's phenotype, including its physical features, metabolism, growth rate, susceptibility to disease, and behavior, are influenced by its genes. As a result, individuals differ from one another, in part because they have different alleles of genes that influence their phenotype. These different alleles arise by **mutation**, a change in the DNA of a gene. Mutations result from events such as copying errors during cell division, mechanical damage when molecules and cell structures collide with DNA, exposure to certain chemicals (called *mutagens*), and exposure to high-energy forms of radiation such as ultraviolet light and X rays. As we'll see in Concept 7.1, the environment can also affect an organism's phenotype. For example, a plant growing in nutrient-rich soil may grow larger than another individual of the same species growing in nutrient-poor soil, even if both have the same alleles of genes that influence size. In this chapter, however, we will focus on phenotypic differences that result from genetic, not environmental, factors.

The formation of new alleles by mutation is critical to evolution. In a hypothetical species in which there was no mutation, each gene would have only one allele, and all members of a population would be genetically identical. If this were the case, evolution could not occur: allele frequencies cannot possibly change over time unless the individuals in a population differ genetically. You may recall from your introductory biology class that the individuals in a population can differ genetically not only because of mutation, but also because of **recombination**, the production of offspring that have combinations of alleles that differ from those in either of their parents. We can think of mutation as providing the raw material (new alleles) on which evolution is based, and recombination as rearranging that raw material into unique new combinations. Together, these processes provide the genetic variation on which evolution depends.

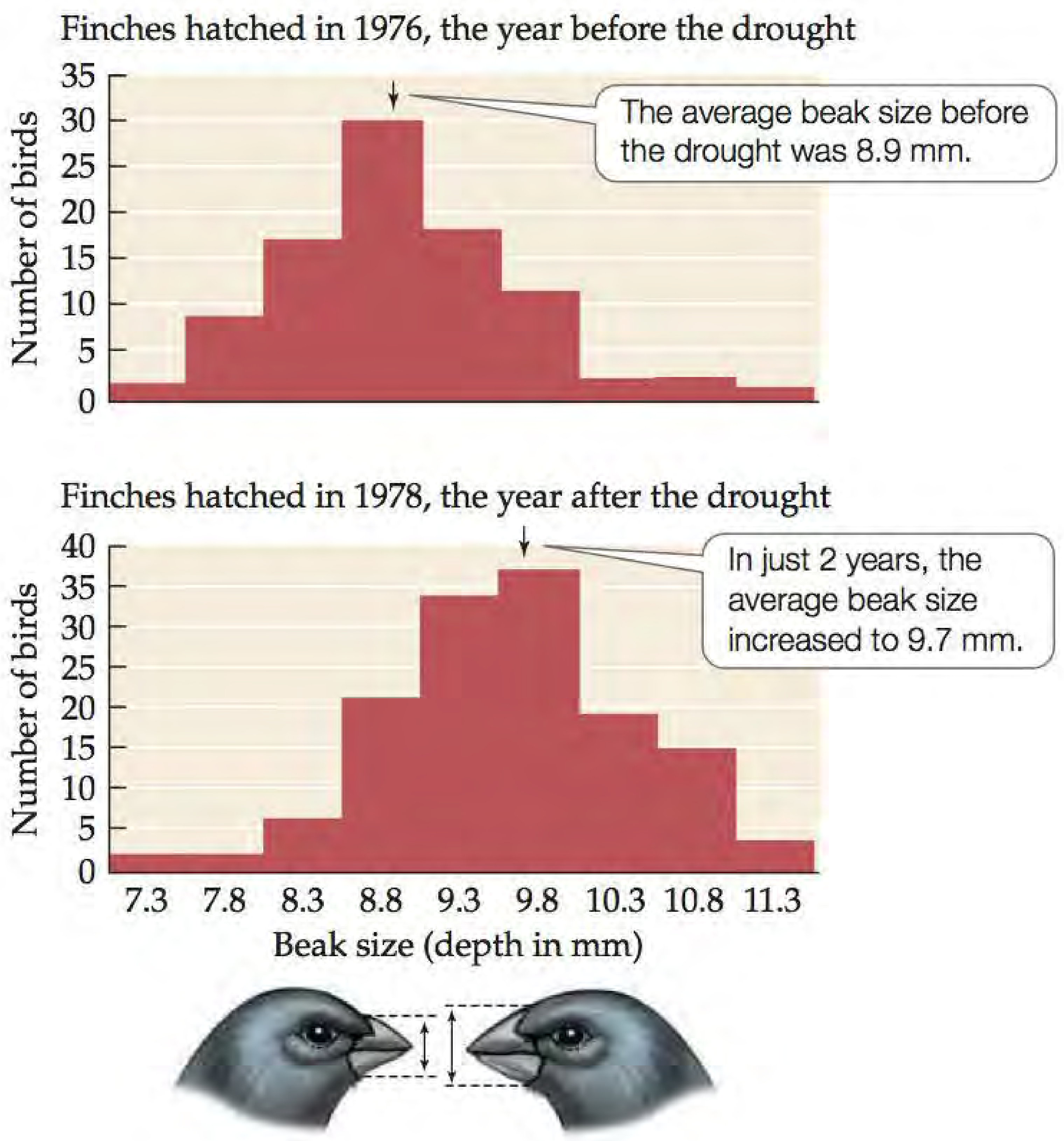
Figure 6.5 Individuals in Populations Differ in Their Phenotypes Poison dart frogs (*Dendrobates tinctorius*) show great variation in color and pattern. Native to northern South America, these frogs live in isolated patches of forest. Their bright colors are thought to serve as a warning to predators of a poison excreted from their skin. Individual frogs likely also differ in other morphological traits as well as in biochemical, behavioral, and physiological traits.

Despite its importance to evolution, mutation occurs too rarely to be the direct cause of significant allele frequency change over short periods of time. Mutations typically occur at rates of 10^{-4} to 10^{-6} new mutations per gene per generation (Hartl and Clark 2007). In other words, in each generation, we can expect one mutation to occur in every 10,000 to 1,000,000 copies of a gene. At these rates, in one generation, mutation acting alone causes virtually no change in the allele frequencies of a population. Eventually, mutation can cause appreciable allele frequency change, but typically it takes thousands of generations for it to do so. Overall, in terms of its direct effects, mutation is a weak agent of allele frequency change. But because it provides new alleles on which natural selection and other mechanisms of evolution can act, mutation is central to the evolutionary process.

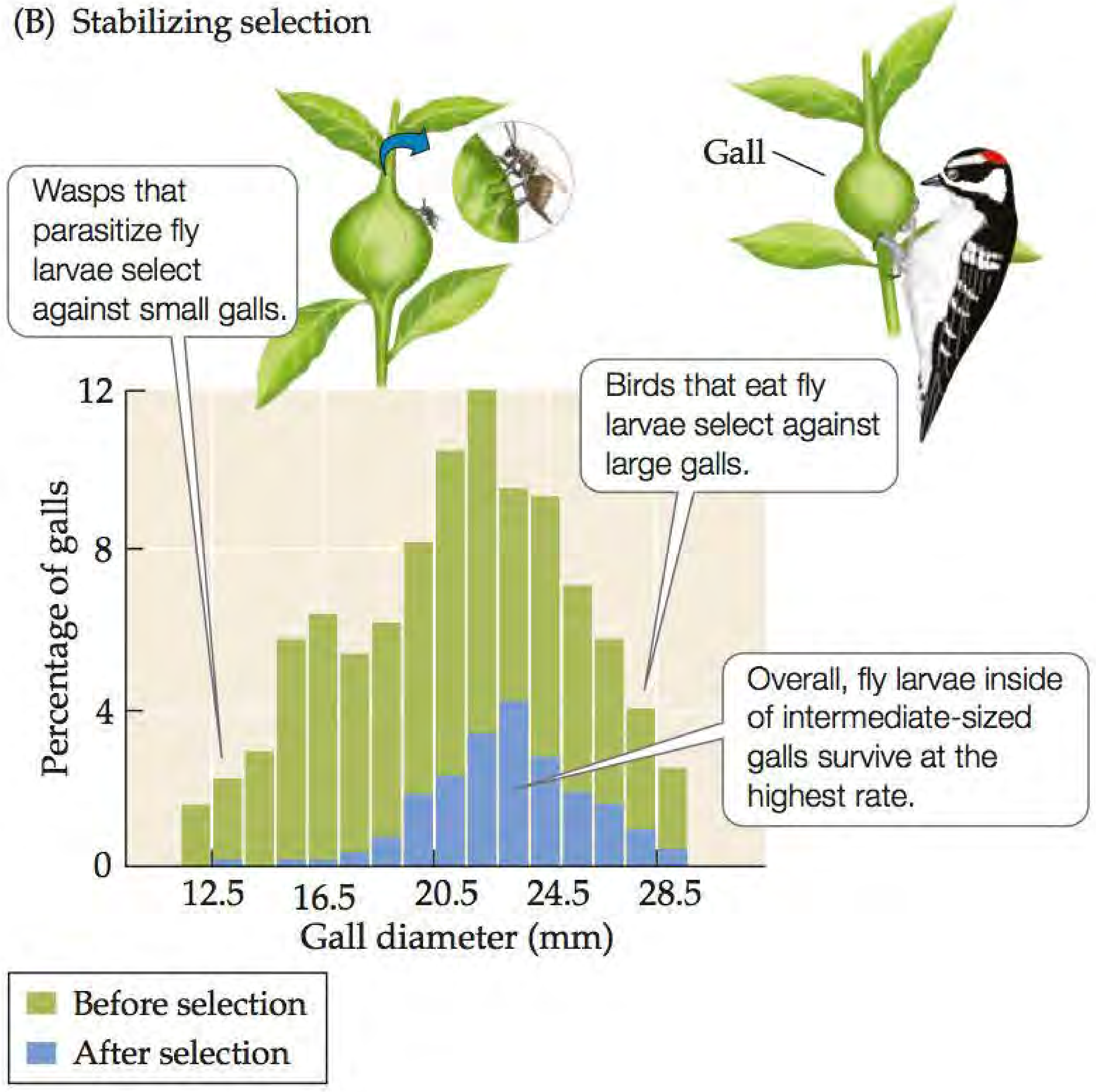
Natural selection increases the frequencies of advantageous alleles

Natural selection occurs when individuals with particular heritable traits consistently leave more offspring than

(A) Directional selection



(B) Stabilizing selection



(C) Disruptive selection

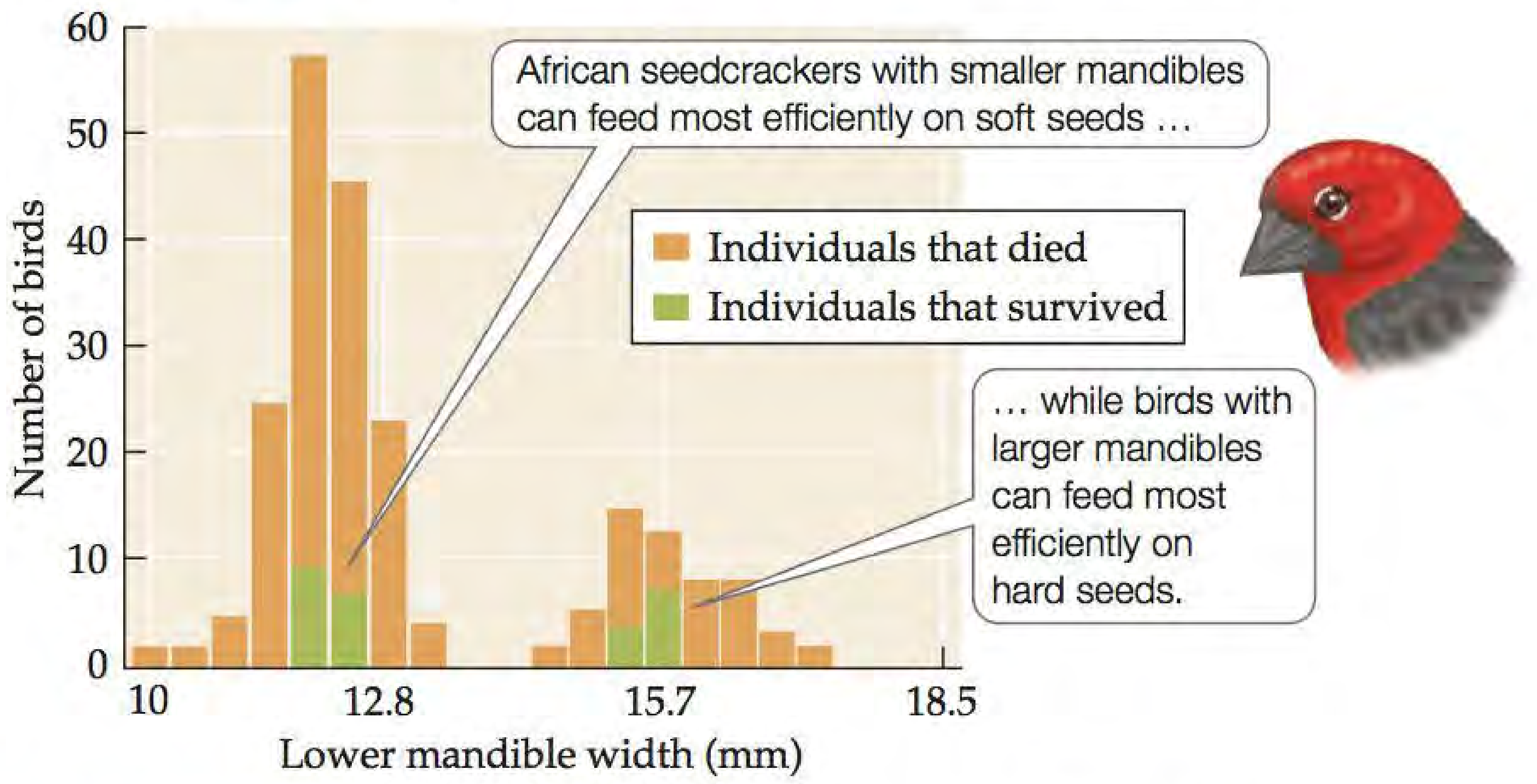


Figure 6.6 Three Types of Natural Selection (A) Directional selection favors individuals at one phenotypic extreme. A prolonged drought in the Galápagos archipelago resulted in directional selection on the beak size of the seed-eating medium ground finch (*Geospiza fortis*). As a result of the drought, most of the available seeds were large and hard to crack, so birds with large beaks, which could more easily crack those seeds, had an advantage over birds with smaller beaks. (B) Stabilizing selection favors individuals with an intermediate phenotype. *Eurosta* flies parasitize goldenrod plants, causing the plant to produce a gall in which the fly larva matures as it feeds on the plant. The preferences of *Eurosta*'s own predators and parasites result in stabilizing selection on gall size. Field observations showed that wasps that parasitize and kill the fly larvae prefer small galls, while birds that eat the fly larvae prefer large galls. As a result, larvae in galls of intermediate size have an advantage. (C) Disruptive selection favors individuals at both extremes. African seedcrackers (*Pyrenestes ostrinus*) depend on two major food plants in their environment. Birds with smaller mandible sizes can feed on one plant's soft seeds most efficiently, while birds with larger mandibles can feed on the other plant's hard seeds most efficiently. Thus, individuals with mandible sizes that are either relatively small or relatively large have an advantage. (A after Grant and Grant 2003; B after Weis and Abrahamson 1986; C after Smith 1993.)

? In (B), do birds or wasps appear to provide stronger selection pressure on gall size? Explain.

do individuals with other heritable traits. But some traits may give organisms an advantage only under certain environmental conditions. Indeed, as we'll see later in this chapter, traits that are advantageous in one environment can be disadvantageous in another.

Depending on what traits are favored, we can categorize natural selection into three types (**Figure 6.6**). **Directional selection** occurs when individuals with one extreme of a heritable phenotypic trait (e.g., large size) are favored over other individuals (small and medium-sized individuals). In **stabilizing selection**, individuals with an intermediate phenotype (e.g., medium-sized individuals) are favored, while in **disruptive selection**, individuals with a phenotype at either extreme are favored (e.g., small and large individuals have an advantage over medium-sized individuals). However, in all three types of natural selection, the fundamental process is the same: some individuals have heritable phenotypes that give them an advantage in survival or reproduction, causing them to leave more offspring than other individuals.

When selection favors a particular phenotype, individuals with alleles that encode that phenotype are likely to leave more offspring than are individuals with other alleles. As a result, alleles that encode a favored phenotype can increase in frequency from one generation to the next. In some cases, the end result of this process is that most or all of the individuals in a population have an allele that encodes a trait favored by selection. A well-studied example is the Andean goose (*Chloephaga melanoptera*), which lives high in the Andes. These birds have evolved a version of the oxygen transport protein hemoglobin that has an unusually high affinity for oxygen and hence provides an advantage in their low-oxygen, high-altitude environment (Weber 2007; McCracken et al. 2009). The allele that encodes this version of hemoglobin occurs at a frequency of 100% in Andean goose populations. An allele such as this that occurs in a population at a frequency of 100% is said to have reached **fixation**.

To recap, natural selection can cause the frequency of an allele that confers an advantage to increase over time, as has occurred in populations of the Andean goose. We'll consider the consequences of such increases in the frequencies of advantageous alleles later in this chapter. But first, we'll look at two other mechanisms that can cause allele frequencies to change: *genetic drift* and *gene flow*.

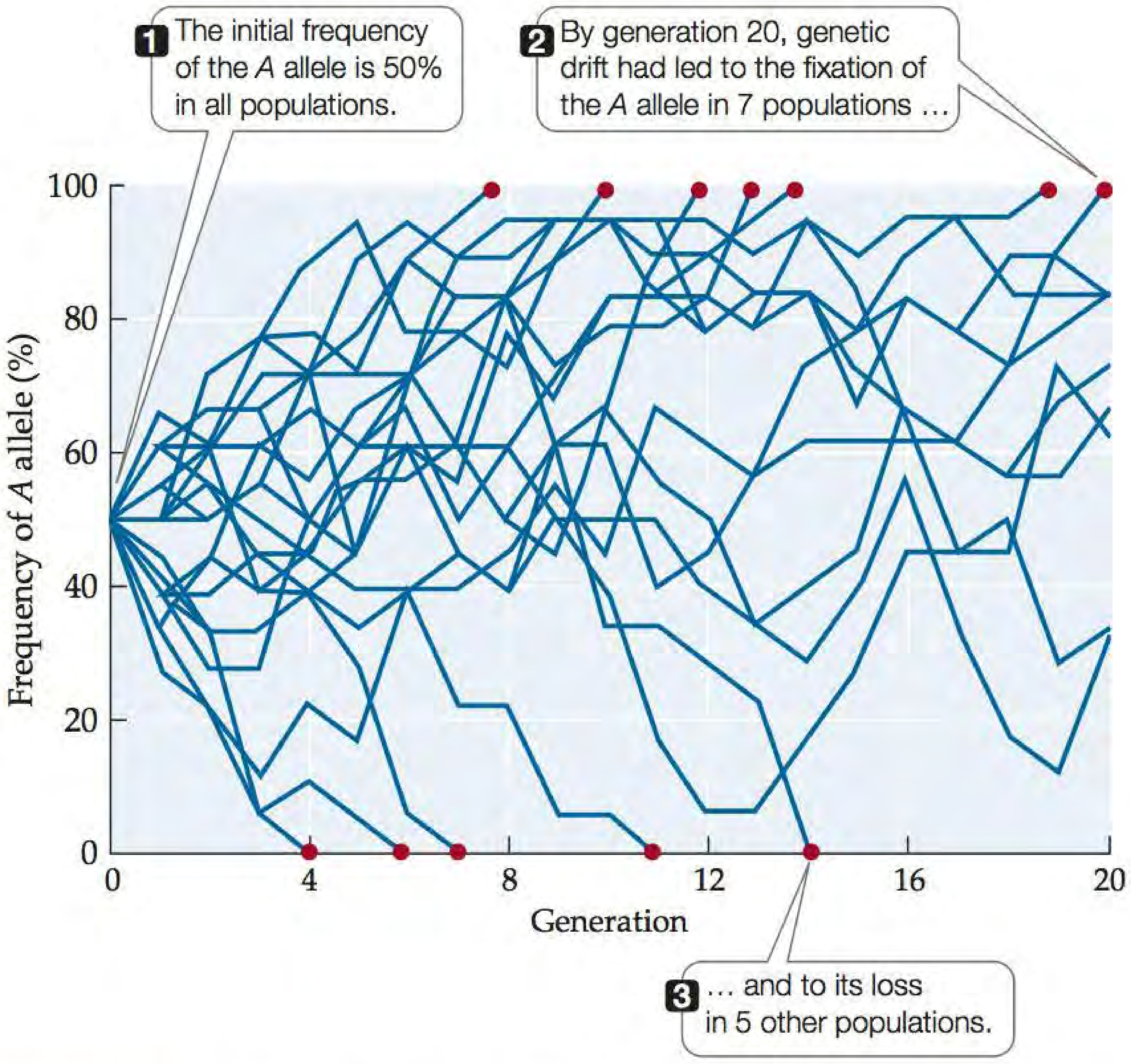
Genetic drift results from chance events

Allele frequencies in populations can be influenced by chance events. Imagine a population of ten wildflowers in which three individuals have genotype *AA*, four have genotype *Aa*, and three have genotype *aa*. Thus, the initial frequency of the *A* allele is 50%, as is the frequency of the *a* allele. Assume that the *A* and *a* alleles encode two different versions of a protein that function equally well. Although neither allele is more advantageous than the other (and hence natural selection does not affect this gene), chance events could alter their frequencies. For example, suppose that a moose walking through the woods happened to step on four of the wildflowers—two of genotype *AA* and two of genotype *Aa*—killing them but not harming any of the three wildflowers of genotype *aa*. As a result, the frequency of the *a* allele in the population would increase from 50% to 67% *by chance alone.*

When chance events affect which alleles are passed from one generation to the next, **genetic drift** is said to occur. Although chance events occur in populations of all sizes, genetic drift alters allele frequencies significantly over short periods only in small populations. To see why, imagine that our wildflower population had 10,000 individuals, 3,000 of genotype *AA*, 4,000 of genotype *Aa*, and 3,000 of genotype *aa*. If (as before) a moose stepped on a random sample of 40% of the individuals in this larger population, there is virtually no possibility that all of the 3,000 individuals of genotype *aa* would be spared. Instead, it is likely that many individuals of each genotype would be killed and, hence, that the frequencies of the *A* and *a* alleles would change little, if at all.

Genetic drift has four related effects on evolution in small populations:

1. Because it acts by chance alone, genetic drift can cause allele frequencies to fluctuate randomly in small populations over time (**Figure 6.7**). When this occurs, eventually some alleles disappear from the population, while others reach fixation.
2. By causing alleles to be lost from a population, genetic drift reduces the genetic variation of the population, making the individuals within the population more similar genetically to one another.



1 The initial frequency of the *A* allele is 50% in all populations.

2 By generation 20, genetic drift had led to the fixation of the *A* allele in 7 populations ...

3 ... and to its loss in 5 other populations.

Figure 6.7 Genetic Drift Causes Allele Frequencies to Fluctuate at Random Results of a computer simulation of genetic drift in 20 populations for a gene with two alleles, *A* and *a*. Each population has nine diploid individuals (18 alleles) each generation. In small populations such as these, genetic drift has rapid effects.

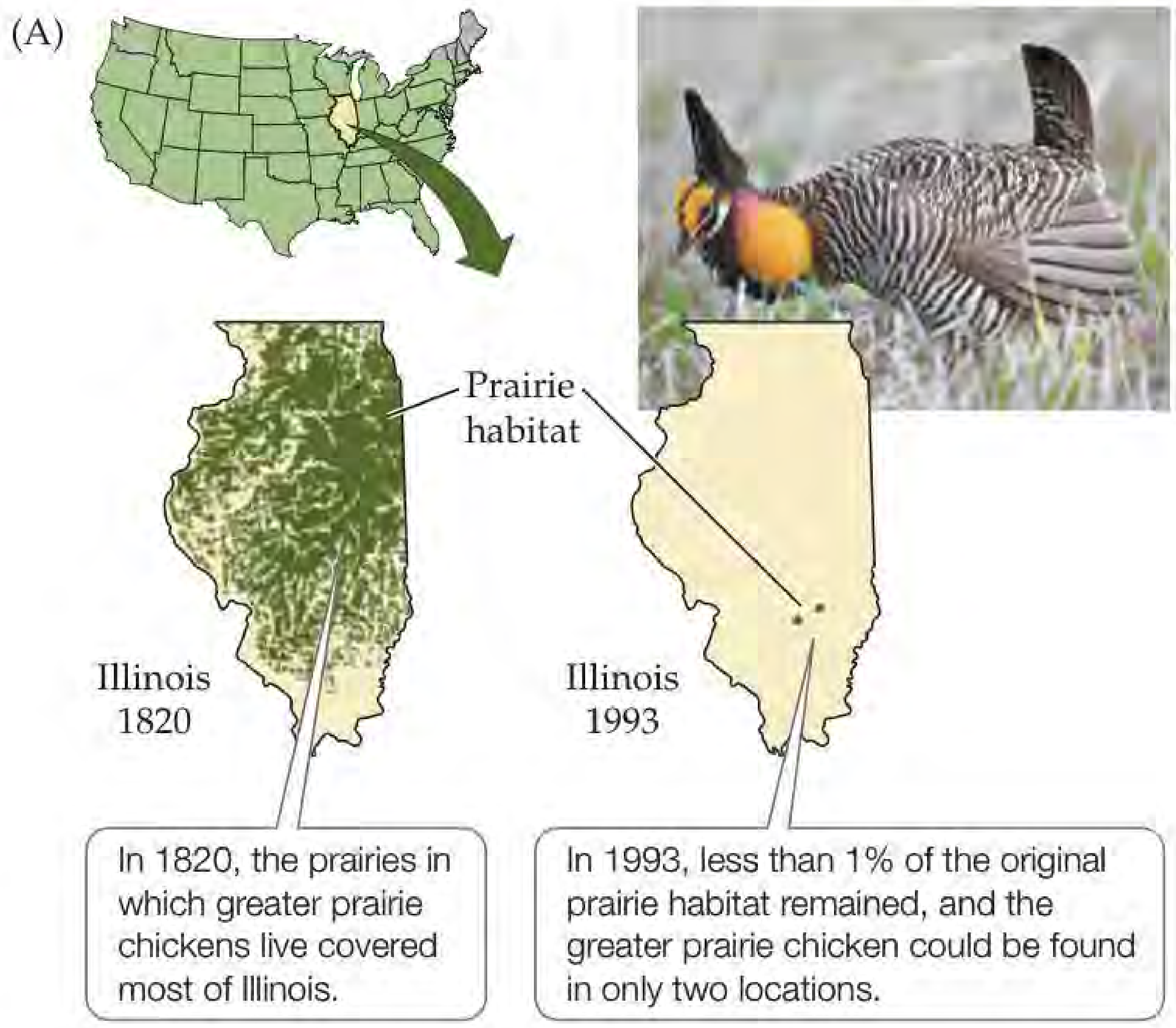
? At the start of the simulation, how many *A* alleles and how many *a* alleles did each population have? At generation 20, how many populations still had both alleles? Predict what would eventually happen to the frequency of the *A* allele in those populations.

3. Genetic drift can increase the frequency of a harmful allele. This may seem counterintuitive because in general, genetic drift acts on alleles that neither harm nor benefit the organism, and we would expect natural selection to reduce the frequency of a harmful allele. However, if the population size is very small and the allele has only slightly deleterious effects, genetic drift can "overrule" the effects of natural selection, causing the harmful allele to increase or decrease in frequency by chance alone.
4. Genetic drift can increase genetic differences between populations because chance events may cause an allele to reach fixation in one population, yet be lost from another population (see Figure 6.7).

The second and third of these effects can have dire consequences for small populations. A loss of genetic variation can reduce the capacity of a population to evolve in response to changing environmental conditions, potentially placing it at risk of extinction. Likewise, an increase in the frequency of harmful alleles in a population can hinder the ability of its members to survive or reproduce, again increasing the risk of extinction. This effect presents an ongoing problem for small populations. Although mutation is unlikely to produce harmful alleles of any particular gene from one generation to the next (because mutations are rare), it is highly likely to produce new deleterious alleles in *some* of an organism's many genes—and genetic drift can cause those alleles to increase in frequency.

Such negative effects of genetic drift are thought to have contributed to the near extinction of the Illinois populations of the greater prairie chicken (*Tympanuchus cupido*). In the early 1800s, there were millions of these birds in Illinois. Over time, their numbers plummeted as more than 99% of the prairie habitat on which they depend was converted to farmland and other uses. By 1993, fewer than 50 greater prairie chickens remained in Illinois. By comparing the DNA of birds in the 1993 Illinois population with that of birds that lived in Illinois in the 1930s (obtained from museum specimens), Juan Bouzat and colleagues (1998) showed that the drop in population size had reduced the genetic variation of the population (**Figure 6.8**). In addition, more than 50% of the eggs laid by birds in the 1993 Illinois population failed to hatch, suggesting that genetic drift had led to the fixation of harmful alleles. This interpretation was strengthened by the results of experiments begun in 1992: when greater prairie chickens from other populations were brought to Illinois, new alleles entered the Illinois population, and egg-hatching rates increased from less than 50% to more than 90% in just 5 years (Westemeier et al. 1998). (Concept 11.3 covers the increased risk of extinction borne by small populations in greater detail.)

(A)



In 1820, the prairies in which greater prairie chickens live covered most of Illinois.

In 1993, less than 1% of the original prairie habitat remained, and the greater prairie chicken could be found in only two locations.

(B)

By 1993, the greater prairie chicken population in Illinois had dropped to fewer than 50 birds and was experiencing the negative effects of genetic drift on small populations.

	ILLINOIS				
	1933	**1993**	**KANSAS**	**NEBRASKA**	**MINNESOTA**
Population size	25,000	<50	750,000	75,000–200,000	4,000
No. of alleles at six genes	31	22	35	35	32
Percentage of eggs that hatch	93	<50	99	96	85

Figure 6.8 Harmful Effects of Genetic Drift (A) As a result of habitat loss, the Illinois population of greater prairie chickens dropped from millions of birds in the 1800s to 25,000 in 1933 and, finally, to fewer than 50 birds in 1993. (B) As the Illinois population shrank in size, genetic drift led to a loss of alleles and to a rise in the frequencies of harmful alleles, thereby reducing egg hatching rates. The table compares the 1993 Illinois populations with historical populations in Illinois and with populations in Kansas, Nebraska, and Minnesota, none of which experienced as severe a drop in population size. (After Bouzat et al. 1998; Westemeier et al. 1998.)

Gene flow is the transfer of alleles between populations

Gene flow occurs when alleles are transferred from one population to another via the movement of individuals or gametes (e.g., plant pollen). Gene flow has two important effects. First, by transferring alleles between populations, it tends to make populations more similar to one another genetically. This homogenizing effect of gene flow is one reason why individuals in different populations of the

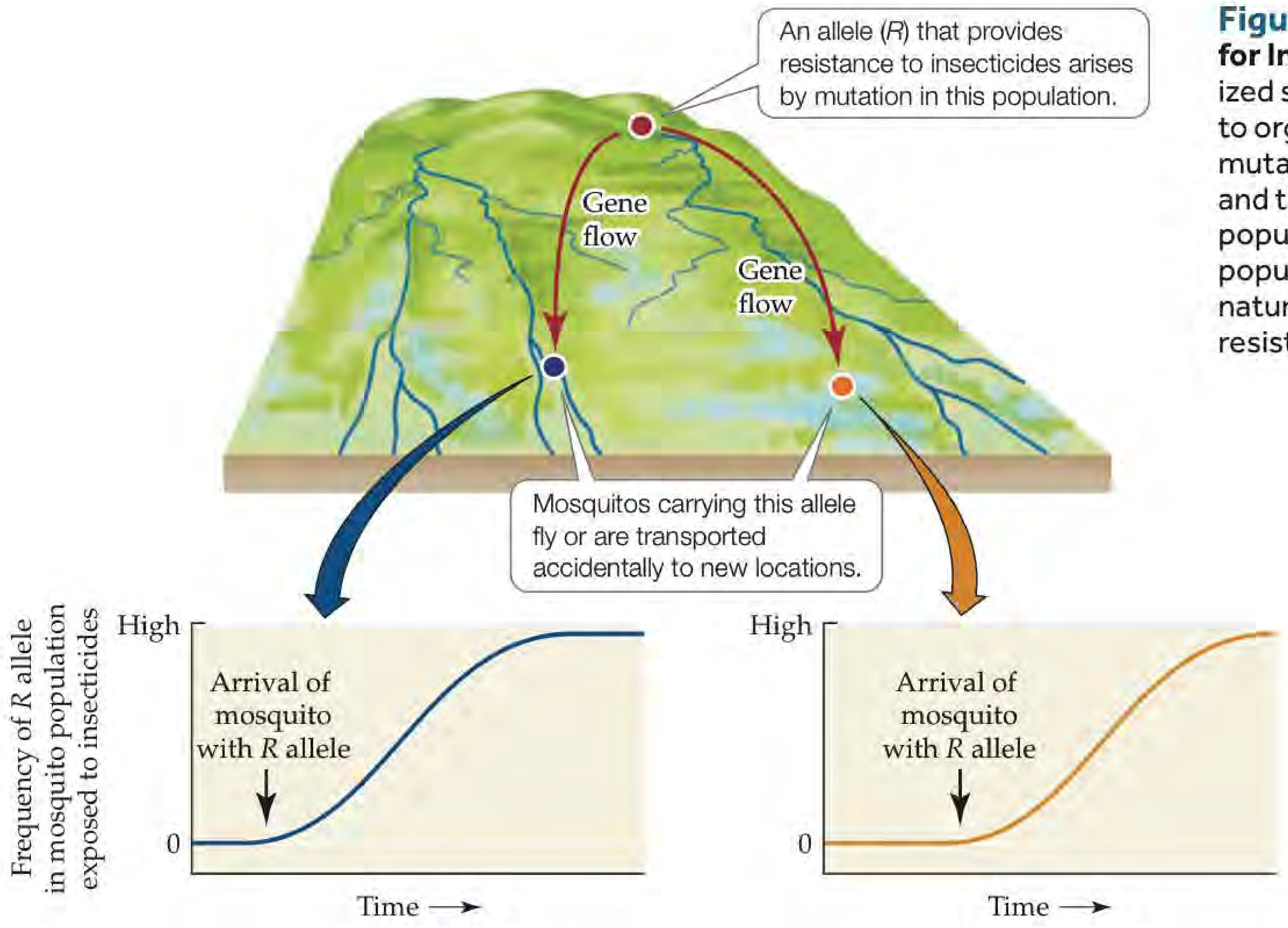


Figure 6.9 Gene Flow: Introducing Alleles for Insecticide Resistance In this idealized scenario, an allele that causes resistance to organophosphate insecticides arises by mutation in one population of mosquitoes and then spreads by gene flow to two other populations. If mosquitoes in those two other populations are exposed to the insecticide, natural selection causes the frequency of the resistance allele to increase rapidly.

same species resemble one another: alleles are exchanged often enough that relatively few differences accumulate between the populations.

Second, gene flow can introduce new alleles into a population. When this occurs, gene flow acts in a manner similar to mutation (although mutation remains the original source of new alleles). This effect of gene flow can have considerable consequences for human health. For example, before the 1960s, the mosquito *Culex pipiens* was not resistant to organophosphate insecticides. This mosquito transmits West Nile virus and other diseases, so insecticides were often used to destroy its populations. In the late 1960s, however, new alleles that provided resistance to organophosphate insecticides were produced by mutation in a few *C. pipiens* populations, probably in Africa or Asia (Raymond et al. 1998). Mosquitoes carrying these alleles were blown by storms or transported accidentally by humans to new locations, where they bred with mosquitoes from the local populations. In populations of mosquitoes exposed to insecticides, the frequency of these introduced alleles then increased rapidly because insecticide resistance was favored by natural selection (**Figure 6.9**). The global spread of these alleles by gene flow has allowed billions of mosquitoes to survive the application of insecticides that otherwise would have killed them.

Evolutionary change that results in a closer match between the traits of organisms and the conditions of their environment, such as the increase in the frequency of insecticide resistance in a *C. pipiens* population exposed to insecticides, is an example of adaptive evolution, the topic we'll consider next.

CONCEPT 6.3

Natural selection is the only evolutionary mechanism that consistently causes adaptive evolution.

Adaptive Evolution

The natural world is filled with striking examples of organisms that are well suited for life in their environments. This match between organisms and their environments highlights their *adaptations*, which are features of organisms that improve their ability to survive and reproduce in their environment (see Concept 4.1). Examples of adaptations include remarkable features like those shown in **Figure 6.10** but also include less visually striking characteristics—such as an enzyme in a desert plant that can function at high temperatures that would denature most enzymes, enabling the plant to thrive in its environment. There are literally millions of other examples of adaptations. How do these adaptations arise?

Adaptations are the result of natural selection

Unlike genetic drift, natural selection is not a random process. Instead, when natural selection operates, individuals with certain alleles consistently leave more offspring than do individuals with other alleles. By consistently favoring individuals with some alleles over individuals with other alleles, natural selection causes **adaptive evolution**, a process of change in which traits that confer survival or reproductive advantages tend to increase in frequency over time. This process tends to

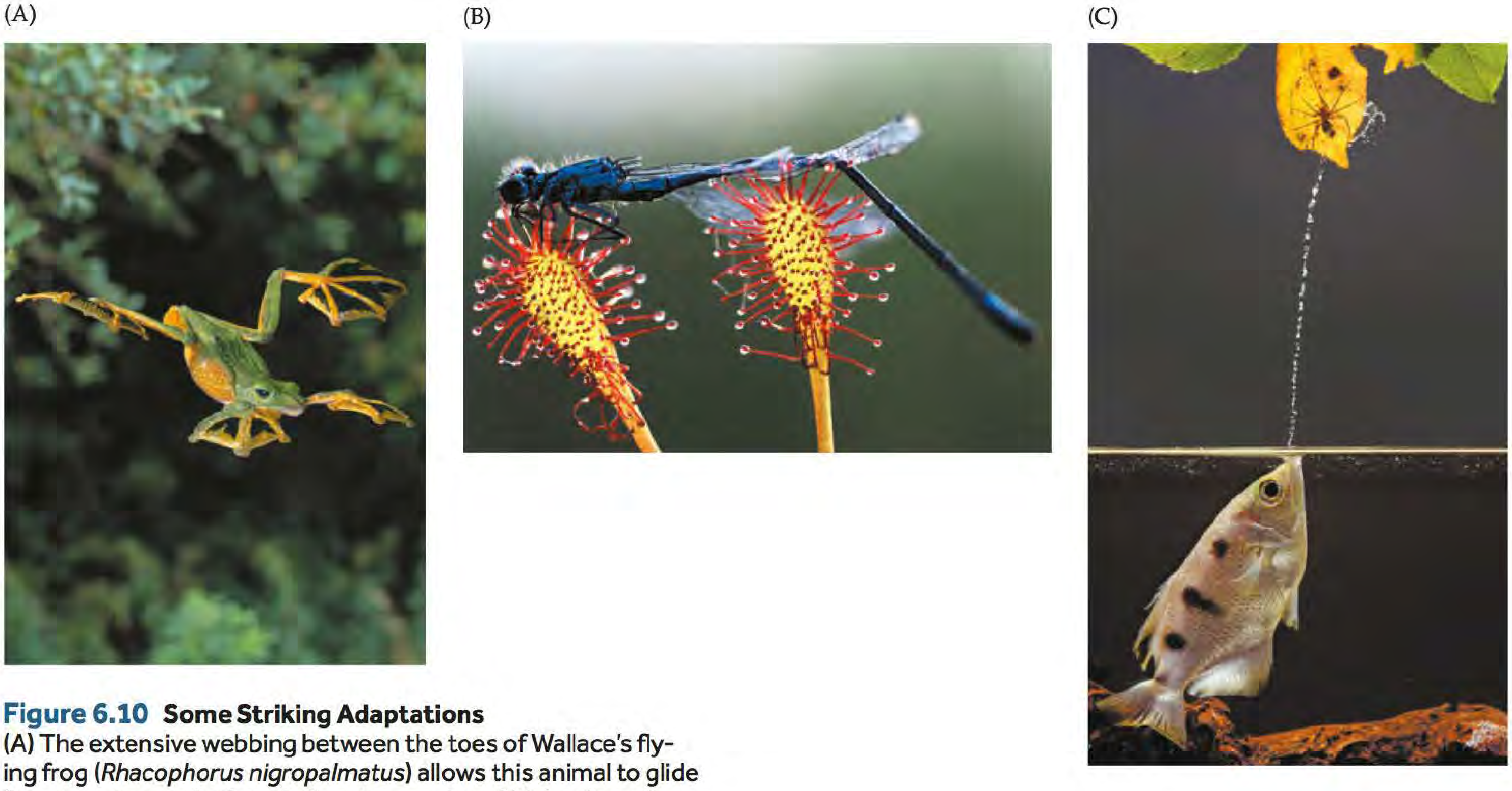


Figure 6.10 Some Striking Adaptations
(A) The extensive webbing between the toes of Wallace's flying frog (*Rhacophorus nigropalmatus*) allows this animal to glide from tree to tree in the rainforest canopies of Malaysia and Borneo. (B) Two oblong-leaf sundew plants (*Drosera intermedia*) with a damselfly caught in a sticky substance the plants secrete from the hairlike structures on the leaves. Sundews, which live in nutrient-poor habitats such as bogs, feed on insects that are attracted to their bright red color and to a sugary solution that coats their leaves. (C) This archerfish (*Toxotes chatareus*) catches a spider by shooting a jet of water into the air. Field observations show that these fish will squirt repeatedly at potential prey and that they can reliably hit targets at heights of up to eight times their body length.

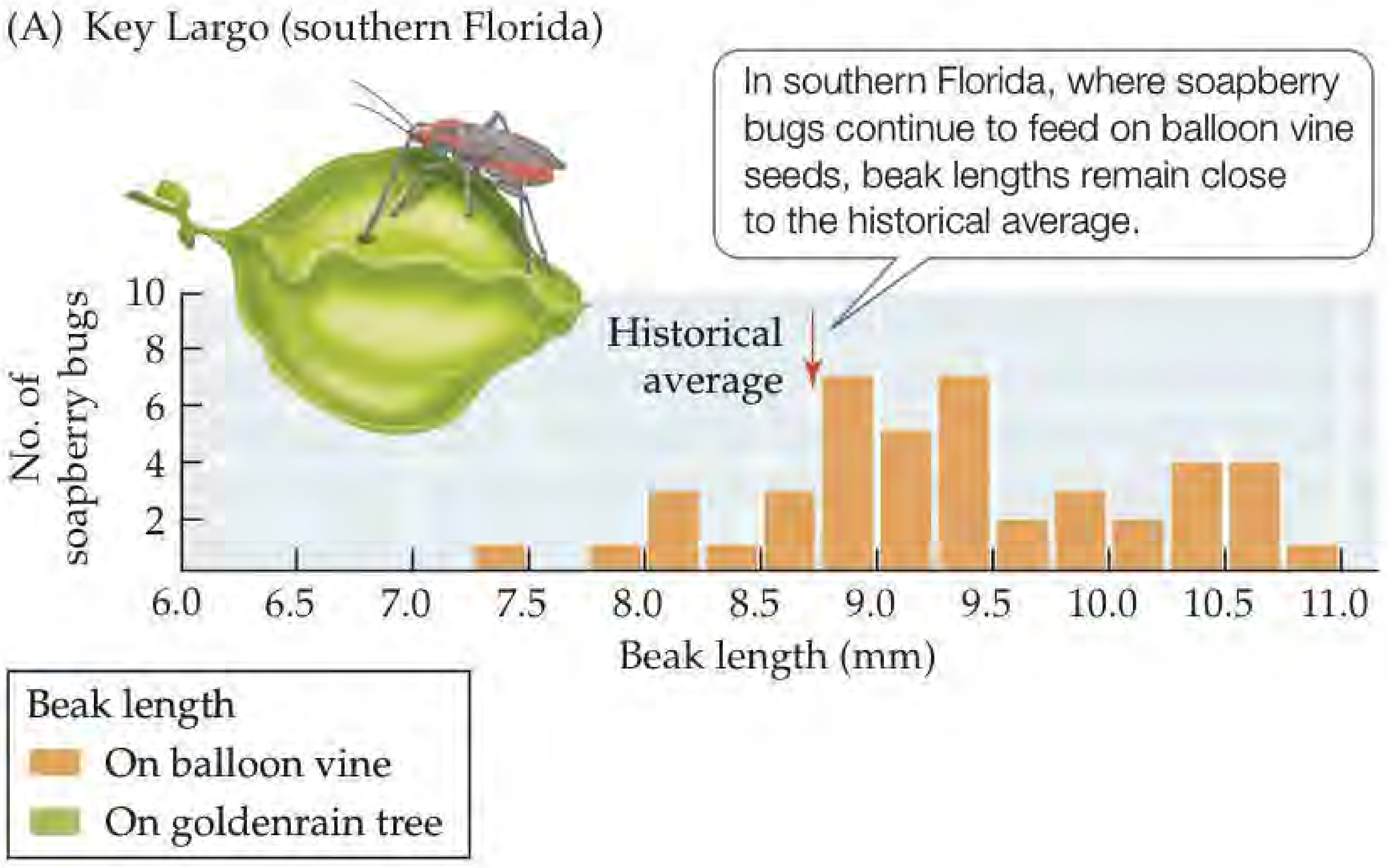
increase the effectiveness of an adaptation that selection acts on, causing the match between organisms and their environments to improve over time. Although gene flow and genetic drift *can* improve the effectiveness of an adaptation (by increasing the frequency of an advantageous allele), they can also do the reverse (by increasing the frequency of a disadvantageous allele). Thus, natural selection is the only evolutionary mechanism that consistently results in adaptive evolution.

An example of adaptive evolution is provided by changes in populations of the soapberry bug (*Jadera haematoloma*) (Carroll and Boyd 1992; Carroll et al. 1997). This insect uses its needle-like beak to feed on seeds located within the fruits of several different plant species. Soapberry bug populations in southern Florida feed on the seeds of the insect's native host, the balloon vine (*Cardiospermum corindum*). Balloon vines, however, are rare in central Florida. Thus, in that region, soapberry bugs do not feed on balloon vines, but instead feed on the seeds of a species introduced from eastern Asia, the goldenrain tree (*Koelreuteria elegans*). A few specimens of the goldenrain tree were brought to Florida in 1926, but it was not commonly planted until the 1950s. The oldest goldenrain trees in the central Florida populations studied by Carroll and colleagues were 35 years old, suggesting that the soapberry bugs there have fed on this species for 35 years or less.

Soapberry bugs feed most efficiently when the length of a bug's beak matches the depth to which it must pierce a fruit to reach the seeds. Since goldenrain tree fruits are smaller than balloon vine fruits, the introduction of the goldenrain tree 35 years ago can be viewed as a natural experiment on the effect of selection on the insect's beak length. Carroll and Boyd predicted that as a result of natural selection, beak lengths would evolve to be *shorter* in soapberry bug populations that fed on goldenrain tree fruits than in populations that fed on the native host, balloon vines. Carroll and Boyd also studied soapberry bugs in Oklahoma and Louisiana, where the insect had begun to feed on several other new host plants that had been introduced within the past 100 years. However, in Oklahoma and Louisiana, the fruits of the introduced hosts were larger than those of the native hosts, leading to the prediction that in those two states, the beak lengths of insects that ate the introduced species would be *longer* than those of insects that ate the native species.

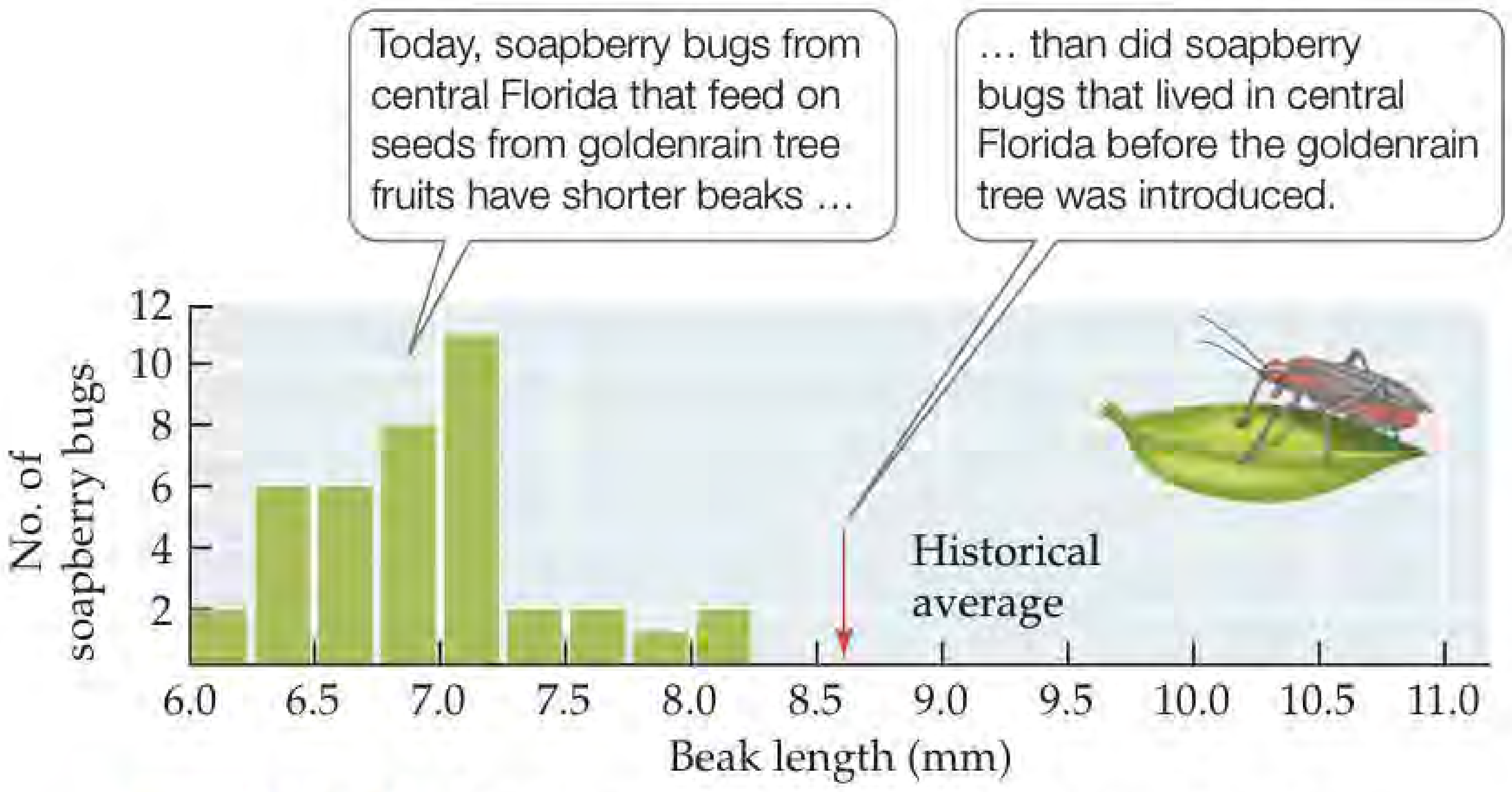
In all three locations, Carroll and Boyd found that soapberry bug beak lengths evolved in the direction

(A) Key Largo (southern Florida)



In southern Florida, where soapberry bugs continue to feed on balloon vine seeds, beak lengths remain close to the historical average.

(B) Lake Wales (central Florida)



Today, soapberry bugs from central Florida that feed on seeds from goldenrain tree fruits have shorter beaks …

… than did soapberry bugs that lived in central Florida before the goldenrain tree was introduced.

Figure 6.11 Adaptive Evolution in Soapberry Bugs Soapberry bug populations in southern Florida feed on the seeds of their native host, the balloon vine (A), while soapberry bug populations in central Florida feed on the seeds of an introduced plant, the goldenrain tree (B). The beak lengths of insects feeding on the goldenrain tree decreased by 26% in 35 years, providing a better match to the smaller fruits of this introduced plant. Red arrows indicate beak length historical averages (obtained from museum specimens collected before the introduction of goldenrain trees). (After Carroll and Boyd 1992.)

predicted by fruit size, decreasing in central Florida (**Figure 6.11**) and increasing in both Oklahoma and Louisiana. The changes in beak length were substantial: compared with historical values, average beak lengths dropped by 26% in central Florida and increased by 8% (on one introduced host species) and 17% (on another introduced host species) in Oklahoma and Louisiana. In addition, Carroll et al. (1997) showed that beak length is a heritable characteristic, so the observed changes in beak length must have been due at least in part to changes in the frequencies of alleles that affect beak length. Thus, we can conclude that in a relatively short time (35–100 years), natural selection in soapberry bug populations caused adaptive evolution in which a characteristic of the organism (beak length) evolved to match an aspect of its environment (fruit size) more closely.

Adaptive evolution can occur rapidly

Soapberry bugs are not unique: studies on populations of a wide range of other organisms show that natural selection can lead to rapid increases in the frequency of advantageous traits. Examples include the evolution of increased antibiotic resistance in bacteria (in days to months); increased insecticide resistance in insects (in months to years); drabber coloration in guppies, which makes them harder for visually hunting predators to find (several years); and increased beak size in medium ground finches (several years; see Figure 6.6A). These and many other examples of apparently rapid evolution are described by Endler (1986), Thompson (1998), and Kinnison and Hendry (2001); collectively, these studies suggest that what we think of as "rapid" evolution may in fact be the norm, not the exception.

CLIMATE CHANGE CONNECTION

Evolutionary Responses to Climate Change Rapid, apparently adaptive evolution also has been documented in response to climate change. Several such studies have focused on **clines**: patterns of change in a characteristic of an organism over a geographic region. For example, in the fruit fly *Drosophila melanogaster*, the alcohol dehydrogenase (*Adh*) gene exhibits a cline in which the Adh^S allele decreases in frequency as latitude increases (**Figure 6.12A**). This pattern has been found in both the Northern and Southern Hemispheres. Previous studies indicated that this cline results from natural selection on the Adh^S allele, which is less effective in the colder temperatures at higher latitudes and hence is less common there.

Over a 20-year period in coastal Australia, the *Adh* cline shifted about 4° in latitude toward the South Pole (Umina et al. 2005), a movement of roughly 400 km (**Figure 6.12B**). During the same period, mean temperatures in the region increased by 0.5°C. Since the Adh^S allele is favored at higher temperatures, the 4° shift in latitude appears to have been a rapid, adaptive increase in the frequency of this allele in response to climate change. As we describe in **Web Extension 6.2**, rapid evolutionary changes that are correlated with global warming have also been observed in worldwide populations of another fruit fly species, *Drosophila subobscura* (Balanyá et al. 2006). Evolutionary responses to climate change over short periods have also been documented in pitcher-plant mosquitoes (Bradshaw and Holzapfel 2001), red squirrels (Réale et al. 2003), tawny owls (Karell et al. 2011), tufted knotweed (Sultan et al. 2013), and the mustard plant *Brassica rapa* (Franks et al. 2007).

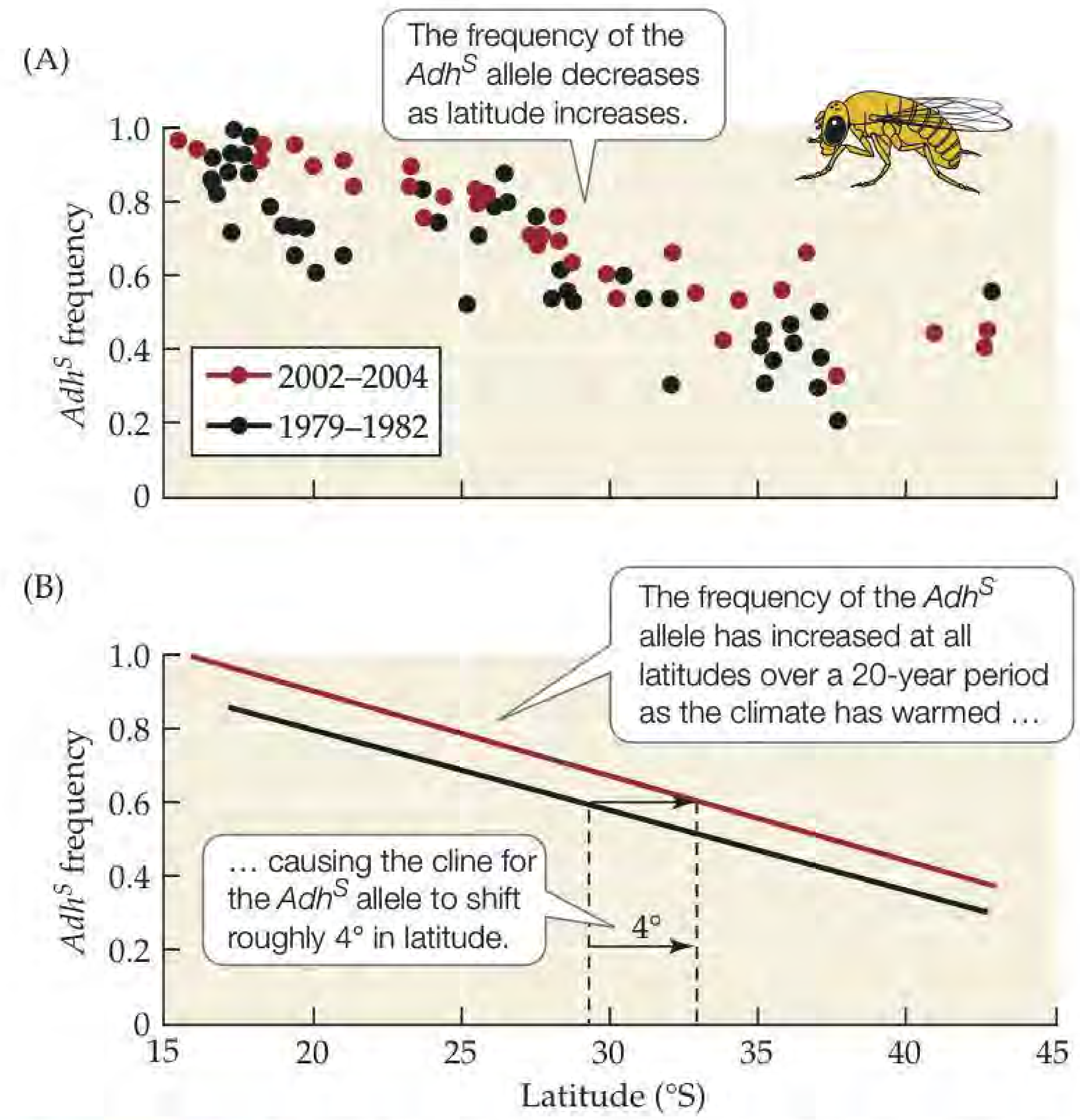


Figure 6.12 Rapid Adaptive Evolution on a Continental Scale The *Adh* gene encodes a metabolically important enzyme, alcohol dehydrogenase, used to detoxify alcohol. Previous field and laboratory studies indicate that the Adh^S allele of this gene is selected against in cooler environments, such as those found at high latitudes. (A) Frequencies of the Adh^S allele in coastal Australian *Drosophila melanogaster* populations in 1979–1982 and in 2002–2004. (B) Regression lines calculated from the data in part A show that between 1979–1982 and 2002–2004, the cline of the Adh^S allele shifted 4° toward the South Pole as the region's average temperatures increased by 0.5°C. (After Umina et al. 2005.)

Finally, hundreds of species have altered the timing of key events in their lives in ways that may be a response to global warming, such as delaying the onset of winter dormancy or reproducing earlier in the spring (Parmesan 2006). In most of these cases, it is not yet known whether the observed changes are due to *phenotypic plasticity* (in which a single genotype produces different phenotypes in different environments; see Concept 7.1), an evolutionary response (in which the genetic constitution of the population changes over time), or both. Recent research has begun to address this issue. For example, Jill Anderson and colleagues (2012) examined the contributions of phenotypic plasticity and evolution to changes in the flowering time of *Boechera stricta*, a mustard plant native to the U.S. Rocky Mountains. Data from a 38-year field survey of *B. stricta* populations show that the date at which flowers first came into bloom was about 13 days earlier in 2011 than it was in 1973. Both adaptive evolution (flowers opened earlier in populations that experienced warming) and phenotypic plasticity contributed to the earlier flowering times observed for this species. (See **Online Climate Change Connection 6.1** for further discussion of evolutionary responses to climate change.)

Gene flow can limit local adaptation

Although many populations are strikingly well matched to their environments, others are not. Gene flow is one of the factors that can limit the extent to which a population is adapted to its local environment. For example, some plant species have tolerant genotypes that can grow on soils at former mine sites containing high concentrations of heavy metals; such soils are toxic to intolerant genotypes. On normal soils, the tolerant genotypes grow poorly compared with the intolerant genotypes. Thus, we would expect the frequencies of tolerant genotypes to approach 100% on mine soils (where they are advantageous) and 0% on normal soils (where they are disadvantageous). Researchers found that a population of the bentgrass *Agrostis tenuis* growing on mine soils was dominated by tolerant genotypes, as expected. However, a population growing on normal soils downwind from the mine site contained more tolerant genotypes than expected (McNeilly 1968). Bentgrass is wind-pollinated, and each year, pollen from the plants growing on mine soils carried alleles for heavy metal tolerance into the population growing on normal soils, preventing that population from becoming fully adapted to its local conditions. The population growing on mine soils also received pollen from plants growing on normal soils. In this population, however, gene flow had relatively little effect on allele frequencies, because selection against intolerant genotypes was so strong (they survived poorly on mine soils). In general, whenever alleles are transferred between populations that live in different environments, the extent to which adaptive evolution occurs in each population depends on whether natural selection is strong enough to overcome the effects of ongoing gene flow.

Adaptations are not perfect

As we have just seen, gene flow can limit the extent to which a population is adapted to its local environment. But even when gene flow does not have this effect, natural selection does not result in a perfect match between organisms and their environments. In part, this occurs because an organism's environment is not static—it is a moving target because the abiotic and biotic components of the environment change continually. In addition, organisms face a number of constraints on adaptive evolution:

- *Lack of genetic variation*. If none of the individuals in a population has a beneficial allele of a particular gene that influences survival and reproduction, adaptive evolution cannot occur at that gene. For example, the mosquito *Culex pipiens* initially lacked alleles that provided resistance to organophosphate insecticides (see Figure 6.9). For decades, this lack of genetic variation prevented adaptive evolution in response to insecticides, allowing humans to destroy mosquito populations at will—at least up until the time when insecticide resistance alleles arose by mutation and spread by gene flow. Note that in this and in all other cases, advantageous alleles arise by chance; they are not produced as needed or "on demand."

- *Evolutionary history*. Natural selection does not craft the adaptations of an organism from scratch. Instead, if the necessary genetic variation is present, it works by modifying the traits already present in an organism. Organisms have certain traits and lack others because of their ancestry. It would be advantageous, for example, for an aquatic mammal such as a dolphin to be able to breathe under water. Dolphins lack this capacity, however, in part because of constraints imposed by their evolutionary history: they evolved from terrestrial vertebrates that had lungs and breathed air. Natural selection can bring about great changes, as seen in the mode of life and streamlined body form of the dolphin, but it does so by modifying traits that are already present in the organism, not by creating advantageous traits de novo.
- *Ecological trade-offs*. To survive and reproduce, organisms must perform many essential functions, such as acquiring food, escaping predators, warding off disease, and finding mates. Energy and resources are required for each of these essential functions. Hence, as suggested by the maxim "There is no free lunch" (see Table 1.1), organisms face **trade-offs** in which the ability to perform one function reduces the ability to perform another (**Figure 6.13**). Trade-offs occur in all organisms, and they ensure that adaptations will never be perfect. Instead, adaptations represent compromises in the abilities of organisms to perform many different and sometimes conflicting functions.

Despite these pervasive constraints, adaptive evolution is a key component of the evolutionary process. What does the importance of adaptive evolution tell us about the link between ecology and evolution? As we saw in the case of soapberry bug populations (see Figure 6.11), natural selection, and the adaptive evolution that results, is driven by the interactions of organisms with one another and with their environment. Any such interaction is an ecological interaction, and hence ecology serves as a basis for understanding natural selection. Next, we'll consider how ecological interactions influence broader evolutionary changes, such as the formation of new species and the great changes that have occurred during the history of life on Earth.

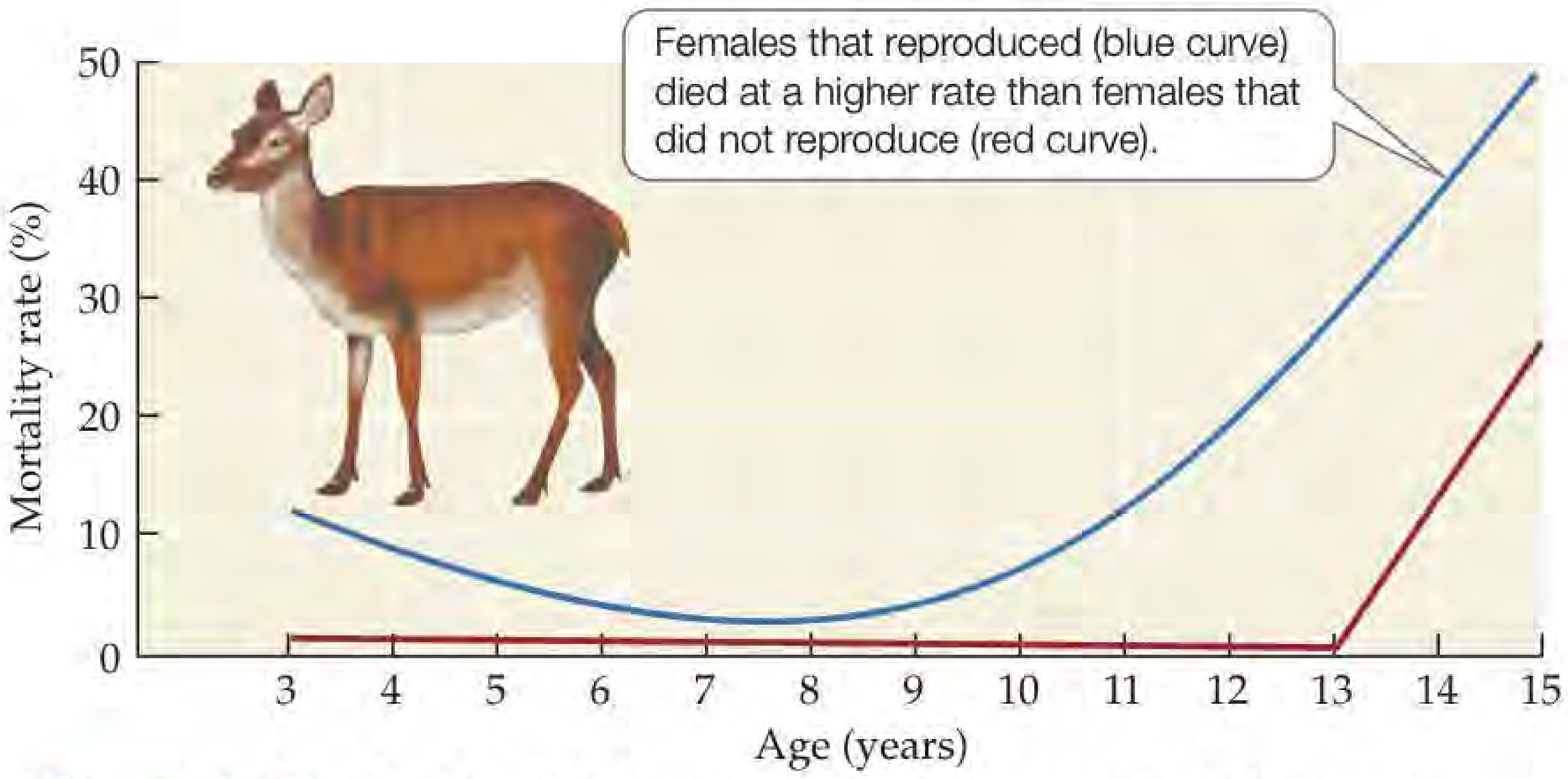


Figure 6.13 A Trade-Off between Reproduction and Survival Female red deer that reproduced had a lower chance of surviving to the next year than did females that did not reproduce. (After Clutton-Brock et al. 1983.)

? Is the additional risk of mortality that results from reproduction the same for females of all ages? Explain.

CONCEPT 6.4

Long-term patterns of evolution are shaped by large-scale processes such as speciation, mass extinction, and adaptive radiation.

The Evolutionary History of Life

Earth is home to roughly 1.5 million species[2] that have been named by taxonomists and to millions more that have yet to be discovered or named. This tremendous diversity serves as a foundation for all of ecology, which, as we saw in Concept 1.2, is the study of how species interact with one another and with their environment. But the causation runs both ways: while it is true that ecological interactions are affected by the diversity of species, it is also true that the diversity of species is shaped by ecological interactions. To see why, let's examine the origin of species and some of the other processes that have affected the history of life on Earth.

The genetic divergence of populations over time can lead to speciation

Each of the millions of species alive today originated by **speciation**, the process by which one species splits into two or more species. Speciation most commonly occurs when a barrier prevents gene flow between two or more populations of a species. The barrier may be geographic,

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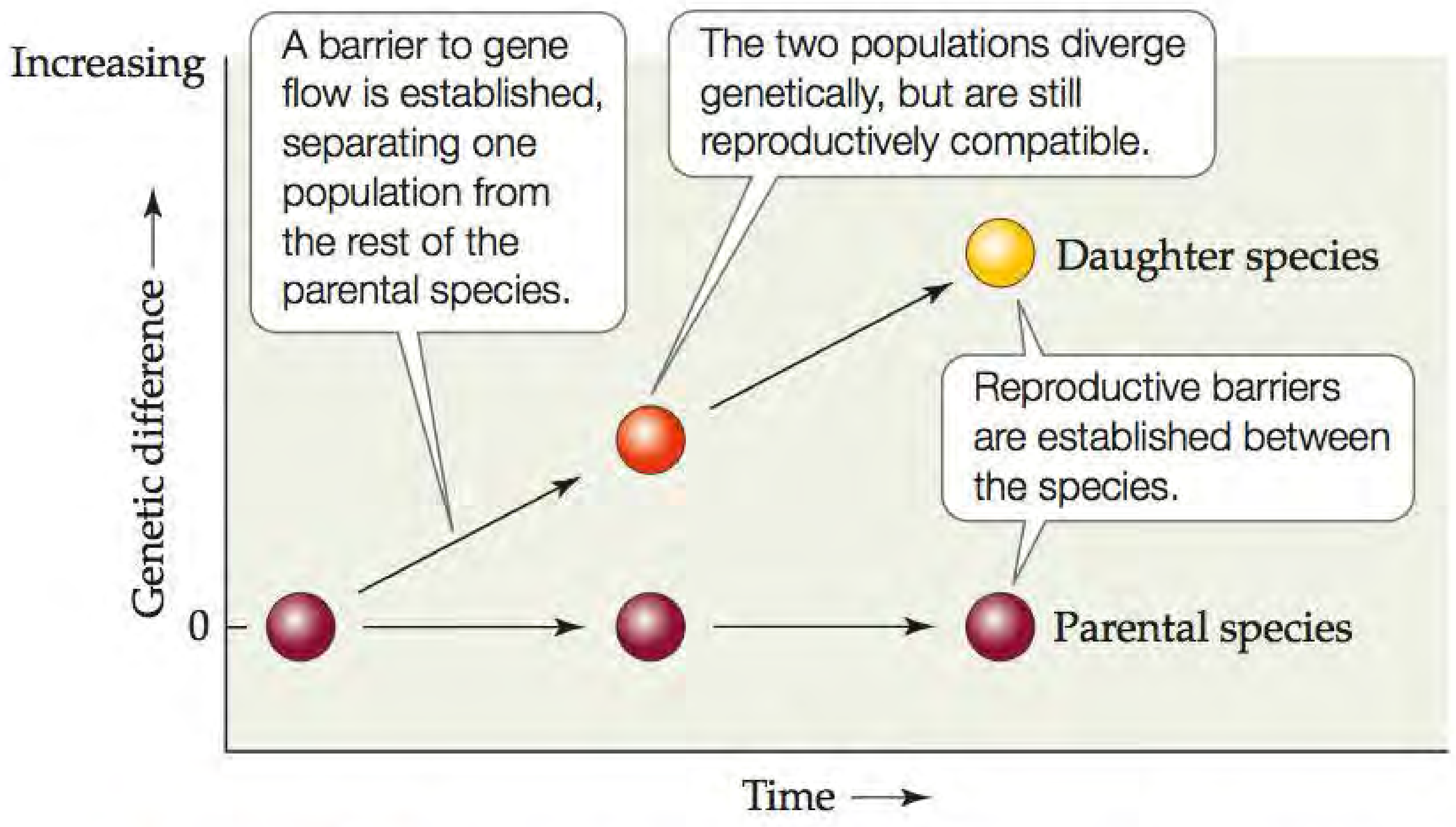
[2] A *species* can be defined as a group of organisms whose members have similar characteristics and can interbreed.



A barrier to gene flow is established, separating one population from the rest of the parental species.

The two populations diverge genetically, but are still reproductively compatible.

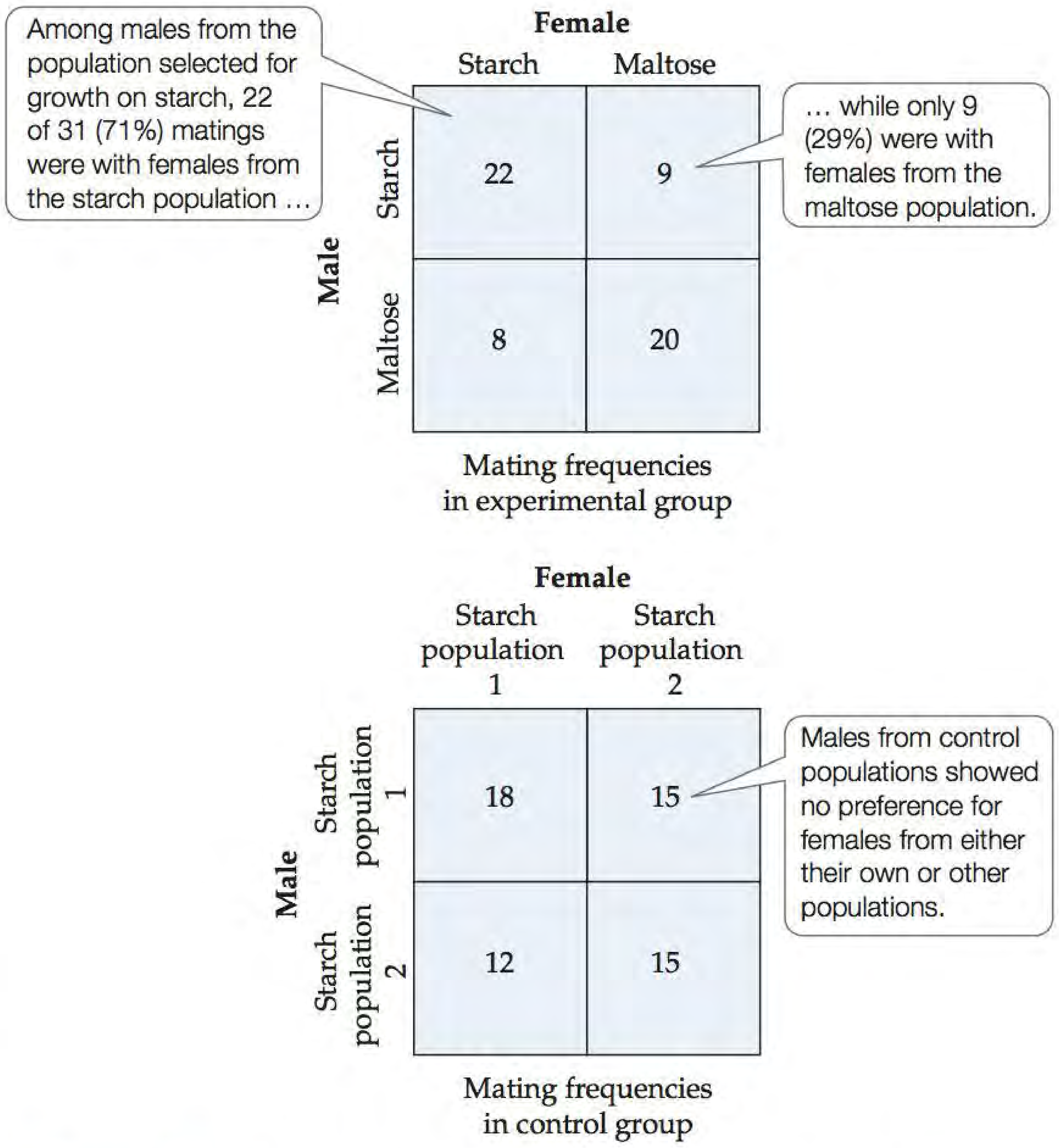
Reproductive barriers are established between the species.

Figure 6.14 Speciation by Genetic Divergence Once genetic divergence begins, the time required for speciation varies tremendously, from a single generation (perhaps a single year), to a few thousand years, to millions of years in most cases.

as when a new population becomes established far from the parental population, or it may be ecological, as when some members of an insect population begin to feed on a new host plant. When a barrier to gene flow is established between populations, they diverge genetically over time (**Figure 6.14**).

New species can also form in several other ways, such as when members of two different species produce fertile hybrid offspring (see Figure 6.21 for an example in sunflowers). Whether it is produced by genetic divergence, hybridization, or other means, the key step in the formation of a new species is the evolution of barriers that prevent its members from breeding freely with members of the parental species. Such reproductive barriers arise when a population accumulates so many genetic differences from the parental species that its members rarely produce viable, fertile offspring if they mate with members of the parental species.

The accumulation of genetic differences that lead to the formation of a new species can be an incidental by-product of selection. For example, an experiment with fruit flies demonstrated the beginnings of reproductive barriers between populations selected for growth on different sources of food, but no such barriers were observed between control populations that had not been subjected to selection (**Figure 6.15**). Natural selection has produced similar changes in plant populations growing on soils with differing concentrations of heavy metals (Macnair and Christie 1983), in frog populations living in environments with different temperatures (Moore 1957), and in fish populations exposed to low or high levels of predation (Langerhans et al. 2007). In each of these cases, reproductive barriers arose as a by-product of selection in response to a feature of the environment, such as food source, heavy metal concentration, temperature, or presence of predators.



Among males from the population selected for growth on starch, 22 of 31 (71%) matings were with females from the starch population …

… while only 9 (29%) were with females from the maltose population.

Male \ Female	Starch	Maltose
Starch	22	9
Maltose	8	20

Mating frequencies in experimental group

Male \ Female	Starch population 1	Starch population 2
Starch population 1	18	15
Starch population 2	12	15

Mating frequencies in control group

Males from control populations showed no preference for females from either their own or other populations.

Figure 6.15 Reproductive Barriers Can Be a By-Product of Selection After 1 year (about 40 generations) in which experimental populations of *Drosophila pseudoobscura* fruit flies were selected for growth on different sources of food, most matings occurred between flies selected to feed on the same food source. No such mating preference was observed in control populations that were not subjected to selection, regardless of whether the control populations were reared on starch (shown here) or maltose (not shown). To reduce the chance that the food eaten by the larvae would produce a body odor in adults that influenced the results, all flies used in the mating preference tests were reared for one generation on a standard cornmeal medium. (After Dodd 1989.)

Genetic drift can also promote the accumulation of genetic differences between populations (see Figures 6.7 and 6.8). As a result, like natural selection, genetic drift can ultimately lead to the evolution of reproductive barriers and hence to the formation of new species. Gene flow, on the other hand, typically acts to slow down or prevent speciation, because populations that exchange many alleles tend to remain genetically similar to one another, making it less likely that reproductive barriers will evolve.

The diversity of life reflects both speciation and extinction rates

As a result of repeated speciation events, the number of species in a particular group of organisms can increase over time. But the number of species in a group of organisms is also affected by extinction: Indeed, the number of species found in a particular group of organisms increases during periods in which more species are produced by speciation than are lost to extinction and decreases when the reverse is true.

We can visualize the outcome of this process with an **evolutionary tree**, a branching diagram that represents the evolutionary history of a group of organisms. **Figure 6.16A** shows an evolutionary tree for the pinnipeds, a group of aquatic mammals consisting of seals, sea lions, and the walrus. The pinniped common ancestor lived about 20 million years ago, and its descendants include the 34 species of living pinnipeds along with a diversity of extinct species. The walrus group, for example, contains only a single species today—the walrus—but it once contained *Gomphotoria pugnax* and as many as 18 other species, all of which are now extinct.

Extinction can also help us to understand the large morphological differences that occur between some closely related groups of organisms. Seals and other pinnipeds, for example, differ greatly from their closest living relatives, members of the weasel family (the mustelids). However, recently discovered fossils of *Puijila darwini* (Rybczynski et al. 2009), an extinct close relative of the pinnipeds, show that extinct relatives of pinnipeds were similar morphologically to some living mustelids, such as otters (**Figure 6.16B**). Over time, repeated speciation events led to the origin of fully aquatic pinnipeds—but because *P. darwini* and other such species have become extinct, there are no living species that "fill the gap" between living pinnipeds and living mustelids.

Speciation and extinction events also have affected the rise and fall of different groups of organisms over long periods, as we'll see in the next section.

Mass extinctions and adaptive radiations have shaped long-term patterns of evolution

Thus far in this chapter, much of our focus has been on the *process* of evolution—the mechanisms by which evolutionary change occurs. But evolution can also be defined as an observed *pattern* of change. Evolutionary patterns are revealed by observations of the natural world, such as data on the changing allele frequencies of a population over time. Patterns of evolutionary change are also documented in the fossil record, which shows that life on Earth has changed greatly over long periods (**Figure 6.17**).

The earliest known fossils are those of 3.5 billion-year-old bacteria, while the most ancient fossils of complex multicellular organisms are of red algae that lived 1.2

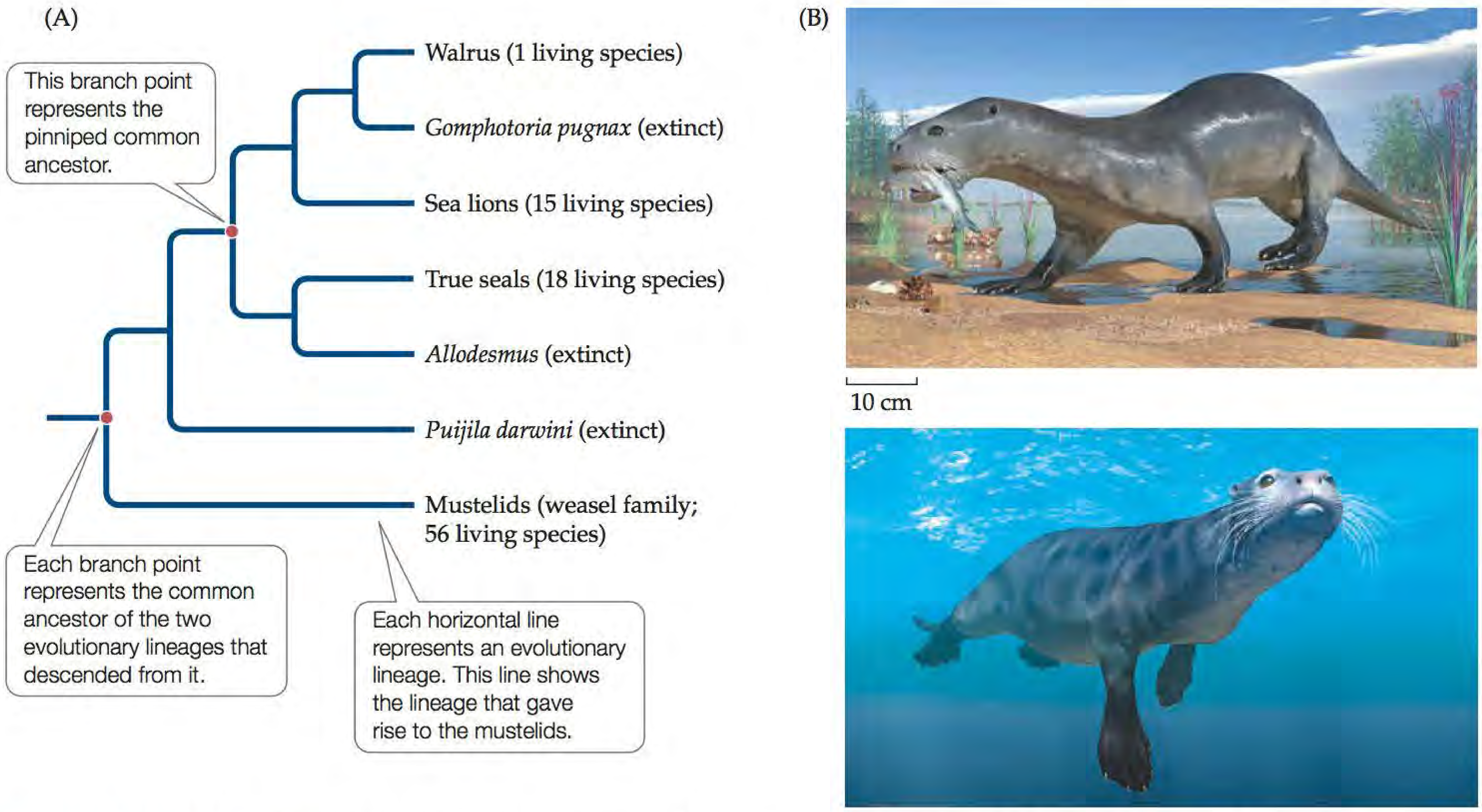
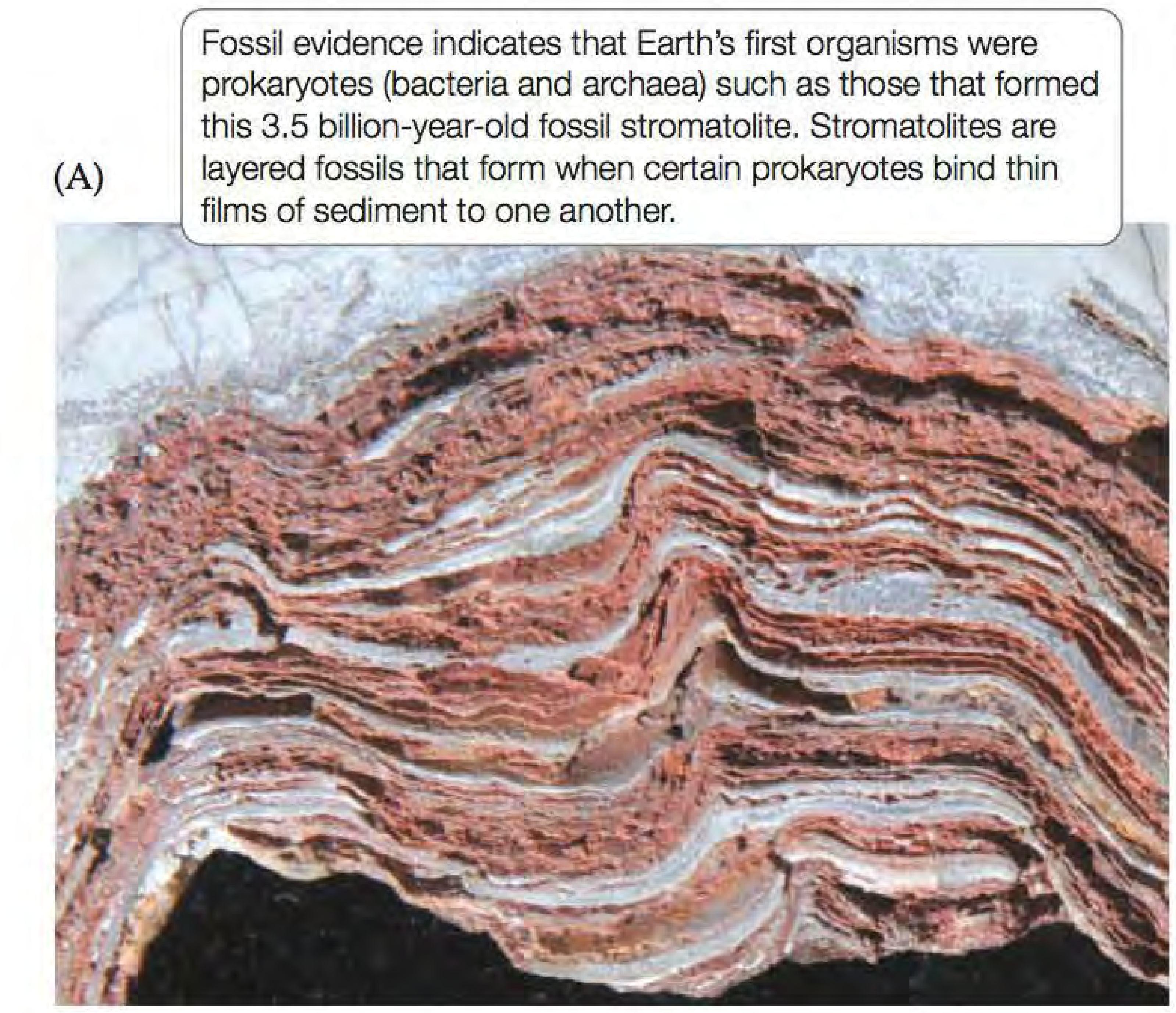
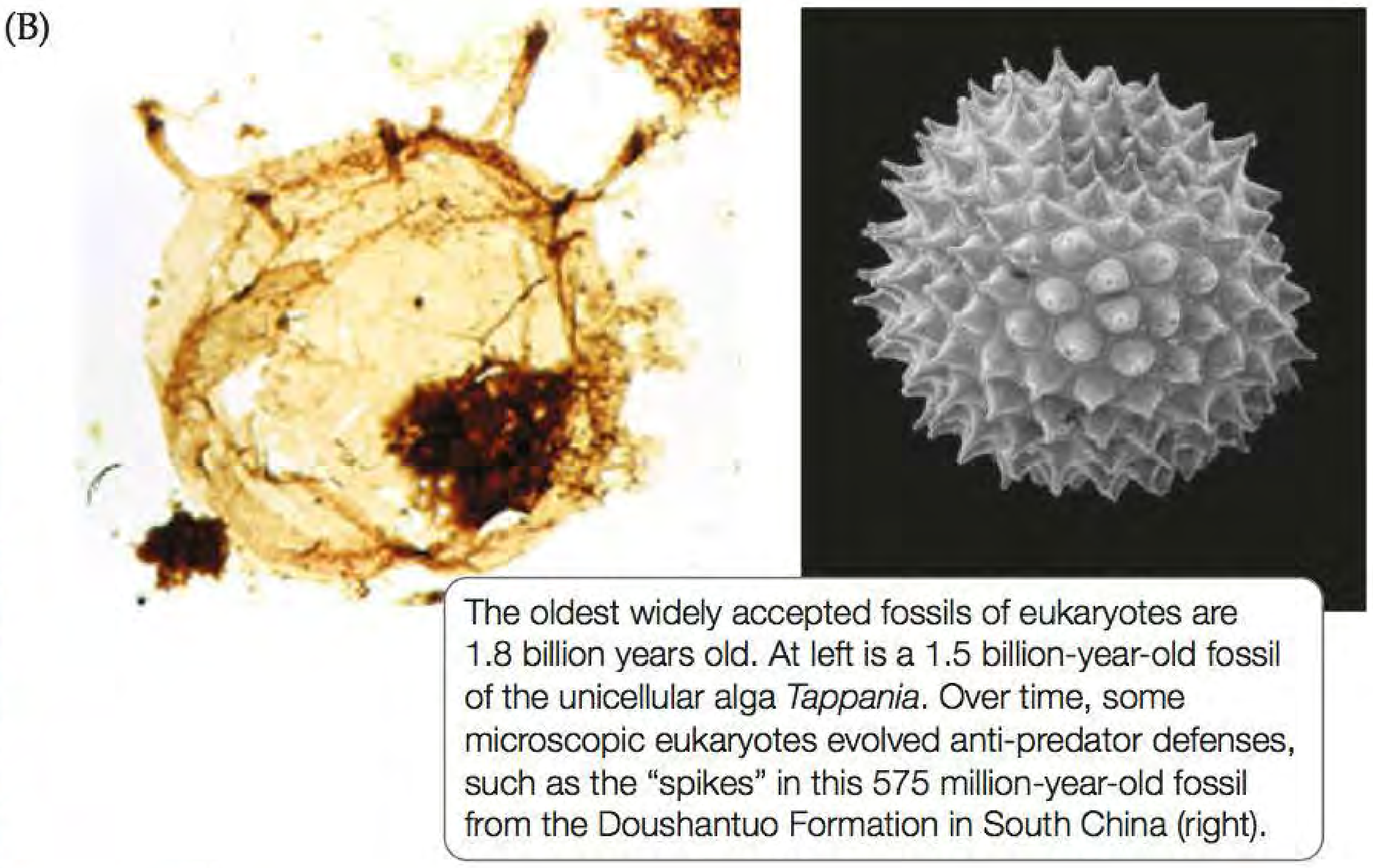


Figure 6.16 An Evolutionary Tree of the Pinnipeds (A) This branching tree is a representation of the evolutionary history of modern seals and their close relatives that is based on recent fossil finds. This research indicates that the marine mammals known as pinnipeds probably share a common ancestor with modern weasels and their relatives. (B) Reconstructions of *Puijila darwini* based on fossils show that extinct close relatives of pinnipeds were similar morphologically to some living mustelids, such as otters. *P. darwini* appears to have foraged both on land (above) and in the water (below). (After Rybczynski et al. 2009; reconstructions courtesy of N. Rybczynski and A. Tirabasso.)

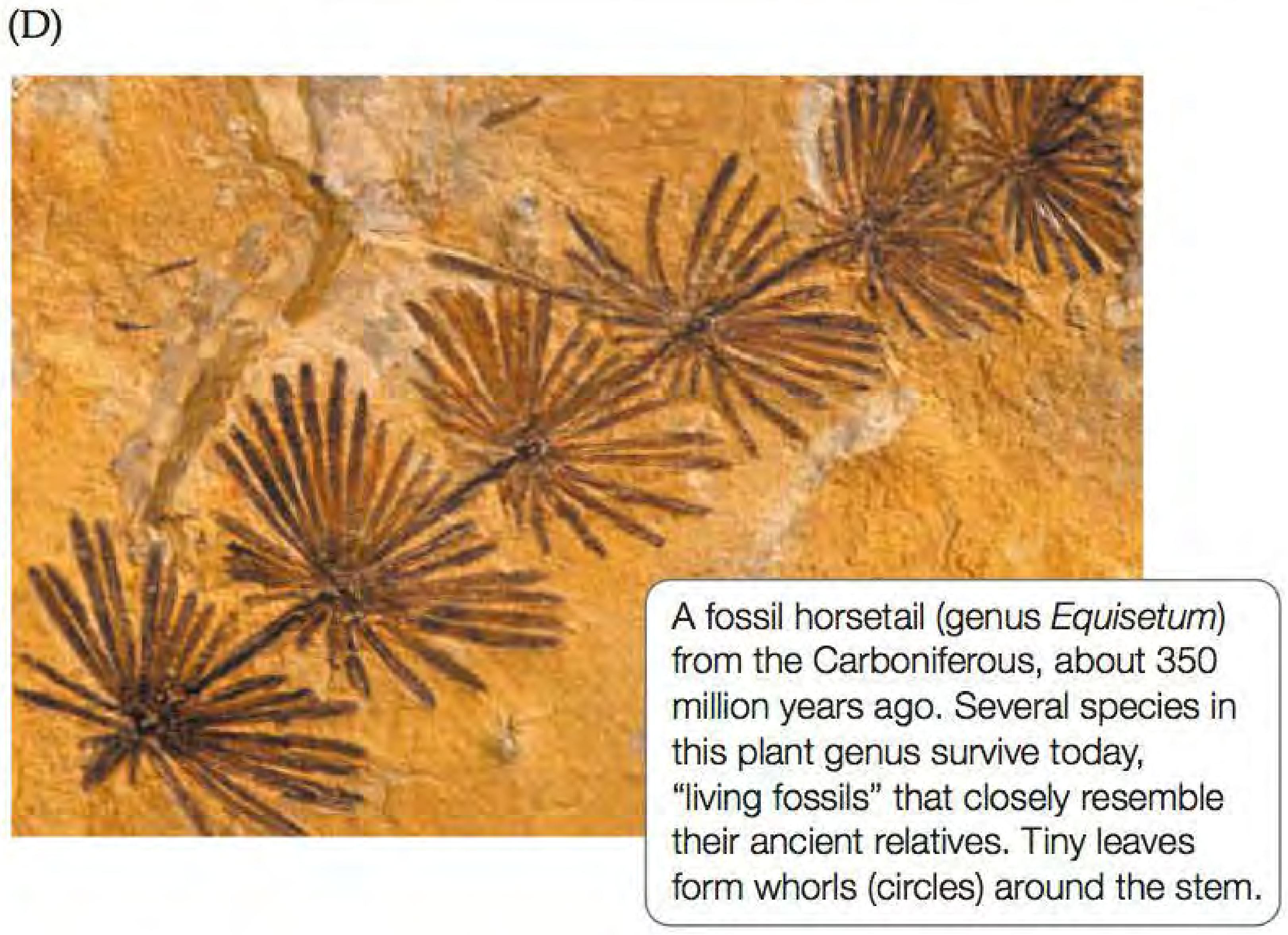


Fossil evidence indicates that Earth's first organisms were prokaryotes (bacteria and archaea) such as those that formed this 3.5 billion-year-old fossil stromatolite. Stromatolites are layered fossils that form when certain prokaryotes bind thin films of sediment to one another.

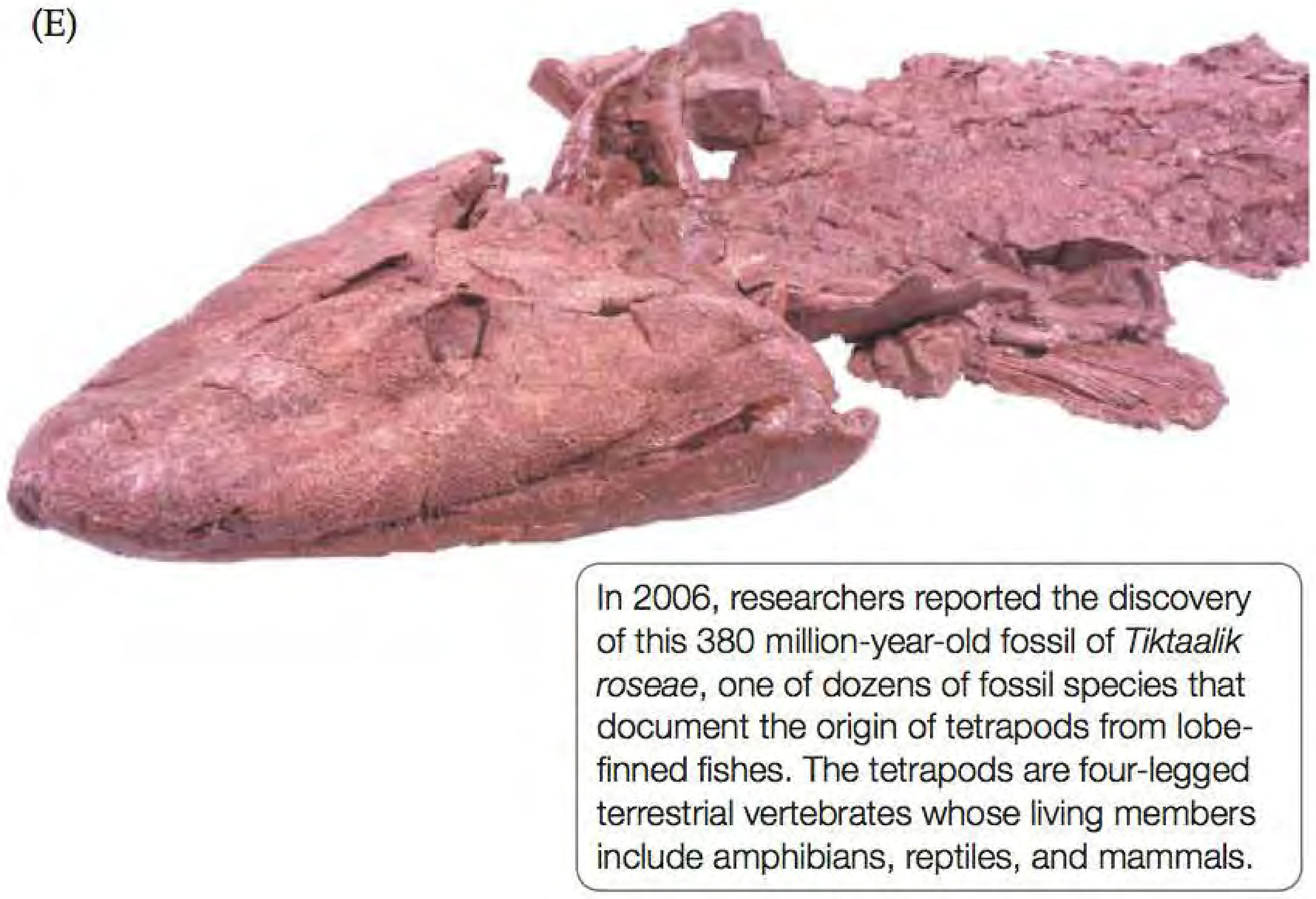


The oldest widely accepted fossils of eukaryotes are 1.8 billion years old. At left is a 1.5 billion-year-old fossil of the unicellular alga *Tappania*. Over time, some microscopic eukaryotes evolved anti-predator defenses, such as the "spikes" in this 575 million-year-old fossil from the Doushantuo Formation in South China (right).

Wiwaxia corrugata was a marine worm, one of many complex animals that originated during the 10 million-year burst of evolutionary activity known as the Cambrian Explosion. This fossil is from the 530 million-year-old Burgess Shale of British Columbia. The artist's reconstruction is a side view and emphasizes the animal's spines.



A fossil horsetail (genus *Equisetum*) from the Carboniferous, about 350 million years ago. Several species in this plant genus survive today, "living fossils" that closely resemble their ancient relatives. Tiny leaves form whorls (circles) around the stem.

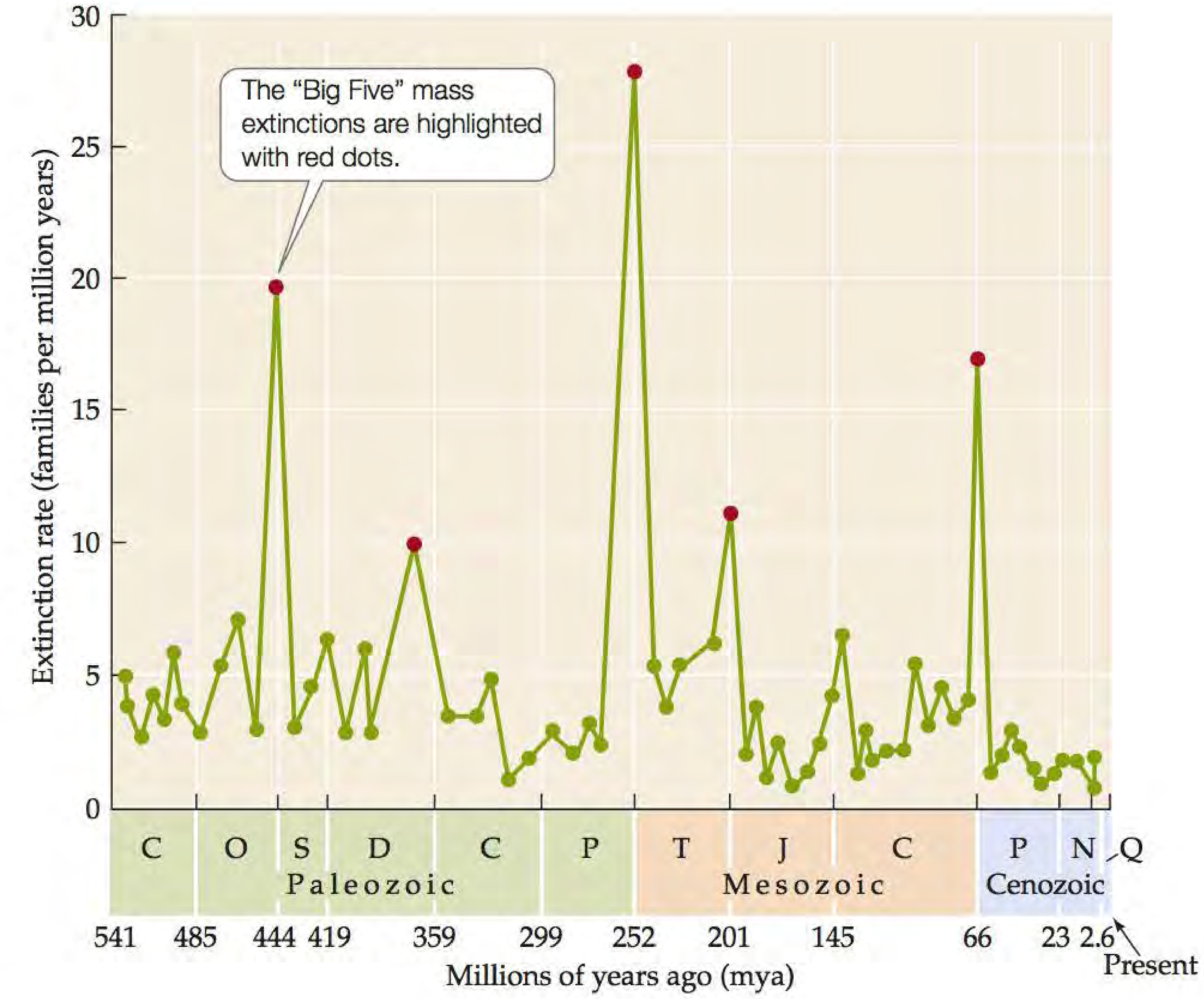


In 2006, researchers reported the discovery of this 380 million-year-old fossil of *Tiktaalik roseae*, one of dozens of fossil species that document the origin of tetrapods from lobe-finned fishes. The tetrapods are four-legged terrestrial vertebrates whose living members include amphibians, reptiles, and mammals.

Figure 6.17 Life Has Changed Greatly over Time

billion years ago. Animals first appear in the fossil record about 600 million years ago, and complex animals with bilateral symmetry (in which the body has two equal but opposite halves, as in most living animals) arose roughly 25 million years later (Fedonkin et al. 2007; Chen et al. 2009). These and many other great changes in the history of life resulted from descent with modification as new species arose that differed from their ancestors. Over millions of years, these differences gradually accumulated, leading eventually to the formation of major new groups of organisms, such as terrestrial plants, amphibians, and reptiles.

For example, a rich variety of fossils have been discovered that illustrate steps in the origin of *tetrapods* (vertebrates with four limbs, a group whose living members include amphibians, reptiles, and mammals) from fishes; the fossil of one such species is shown in Figure 6.17E. Similarly, the fossil record contains dozens of fossil species that show how mammals arose over a 120 million-year period (300 to 180 million years ago) from an earlier group of tetrapods, the synapsids (Allin and Hopson



The “Big Five” mass extinctions are highlighted with red dots.

Figure 6.18 The “Big Five” Mass Extinctions Five peaks in extinction rates are revealed by a graph of extinction rates over time in families of marine invertebrates. (See Figure 2.24 for the full name of each geological period.)

1992; Sidor 2003). The fossil record also documents cases in which the rise to prominence of one group of organisms was associated with the decline of another group. For example, 265 million years ago, reptiles replaced amphibians as the ecologically dominant group of tetrapods, and then, 66 million years ago, the reptiles were replaced in turn by the mammals.

The rise and fall of different groups of organisms over time has been heavily influenced by mass extinctions and adaptive radiations. The fossil record documents five **mass extinction** events in which large proportions of Earth’s species were driven to extinction worldwide in a relatively short time—a few million years or less, sometimes much less (**Figure 6.18**). The most recent mass extinction occurred 66 million years ago and may have been caused by a large asteroid that struck Earth, setting in motion cataclysmic environmental changes that led to the demise of dinosaurs and many other groups of organisms.

Each of the five mass extinctions was followed by great increases in the diversity of some of the surviving groups of organisms; mammals, for example, increased greatly in diversity after the extinction of dinosaurs. Mass extinctions can promote such increases in diversity by removing competitor groups, thus allowing the survivors to give rise to new species that expand into new habitats or new ways of life. Great increases in diversity can also occur when a group of organisms evolves major new adaptations, such as the stems, waxy cuticles, and stomates on leaves that provided early land plants with support against gravity and protection from desiccation (see Concept 4.3). Whether stimulated by a mass extinction, new adaptations, or other factors (such as migration to an island that lacks competitors), an event in which a group of organisms gives rise to many new species that expand into new habitats or new ecological roles in a relatively short time is referred to as an **adaptive radiation**.

What can we learn about ecology and evolution from mass extinctions, adaptive radiations, and other great changes in the history of life? First, biological communities are devastated by mass extinction events (**Figure 6.19**).

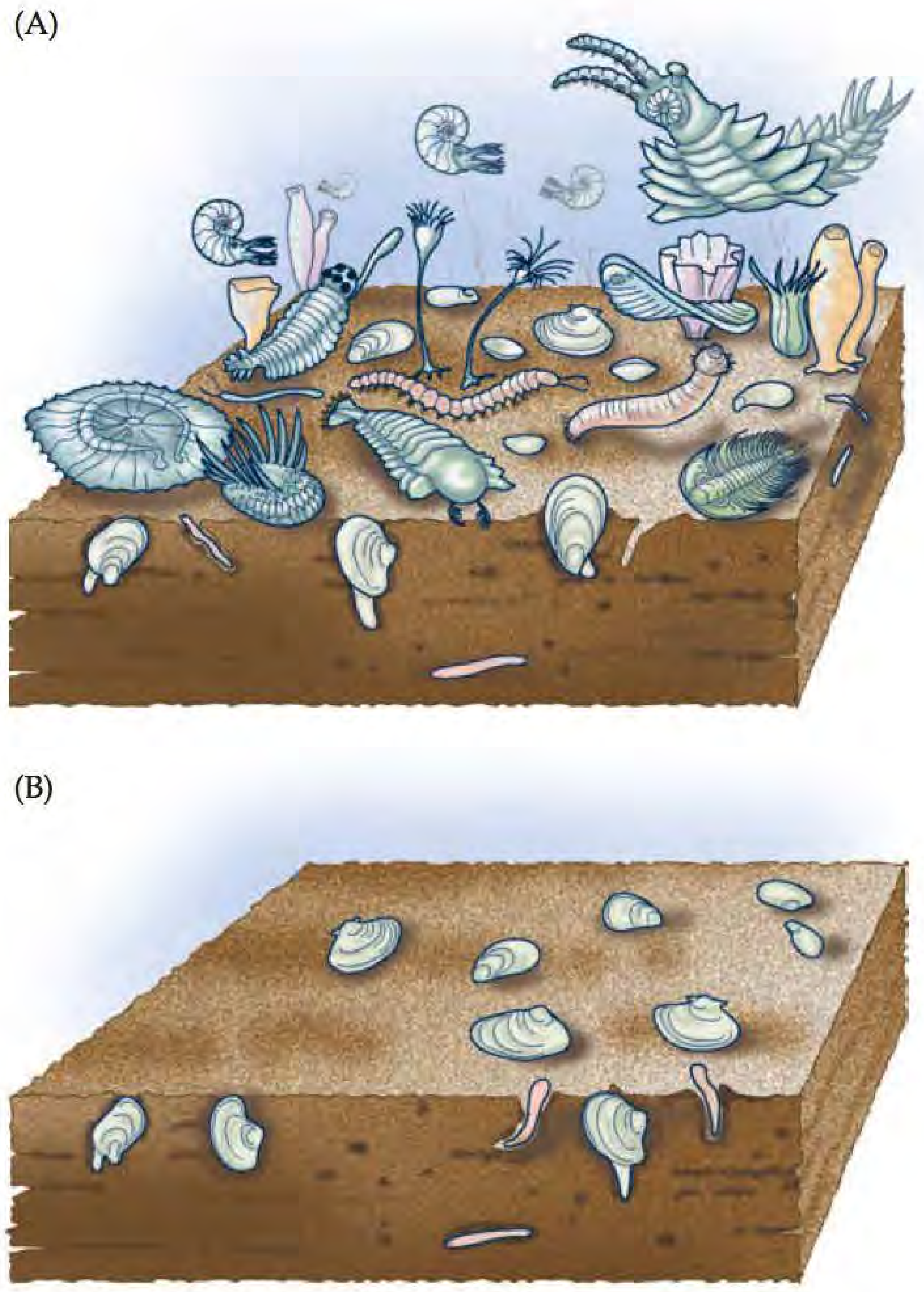


Figure 6.19 Devastating Effects of a Mass Extinction An artist’s rendering of an ancient seabed (A) before and (B) after the end-Permian mass extinction 252 million years ago. Over 90% of marine species were driven to extinction, radically altering this biological community and many others worldwide.

Second, after a mass extinction occurs, it takes millions of years for adaptive radiations to increase the diversity of life to the levels seen prior to the mass extinction (Jablonski 1995). These two observations have sobering implications for the consequences and likely recovery time if human activities cause a sixth mass extinction, as many scientists predict they will do if current trends continue (see Concept 23.3).

Fossil evidence also suggests that many of the great changes in the history of life were caused by ecological interactions. For example, the fossil record shows that for over 60 million years, early animals were small or soft bodied, or both, and that all of the larger species were herbivores, filter feeders, or scavengers. However, beginning 535 million years ago, this safe, soft-bodied world disappeared forever with the appearance of large, well-armed, mobile predators and large, well-defended prey. This major step in the history of life appears to have resulted from an "arms race" between predators and prey. Early predators equipped with claws and other adaptations for capturing large prey provided powerful selection pressure that favored heavily armored prey species. That armor, in turn, promoted further increases in the effectiveness of the predators, and so on. Such reciprocal evolutionary change in interacting species, known as *coevolution*, is discussed in more detail in Concept 13.3.

Ecological interactions have shaped the history of life in many other ways. For example, the origin of new species in one group of organisms can lead to increases in the diversity of other groups, especially those that can escape from, eat, or compete effectively with the new species (Farrell 1998; Benton and Emerson 2007). An example of this process can be seen in parasitic wasps that feed on the apple maggot fly (*Rhagoletis pomonella*), a species that eats fruits (**Figure 6.20**). Following the introduction of apple trees to North America 200 years ago, some *Rhagoletis* populations began to eat apples. As these populations adapted to their new food plant, they diverged from the parent species genetically and now appear to be well on the way to forming a new fly species (Feder 1998). In addition, populations of the wasp have emerged that specialize on the incipient fly species (Forbes et al. 2009). These wasps have become reproductively isolated from the parent wasp species, thereby providing evidence of a sequence of speciation events that is in progress today and appears to be driven by ecological interactions.

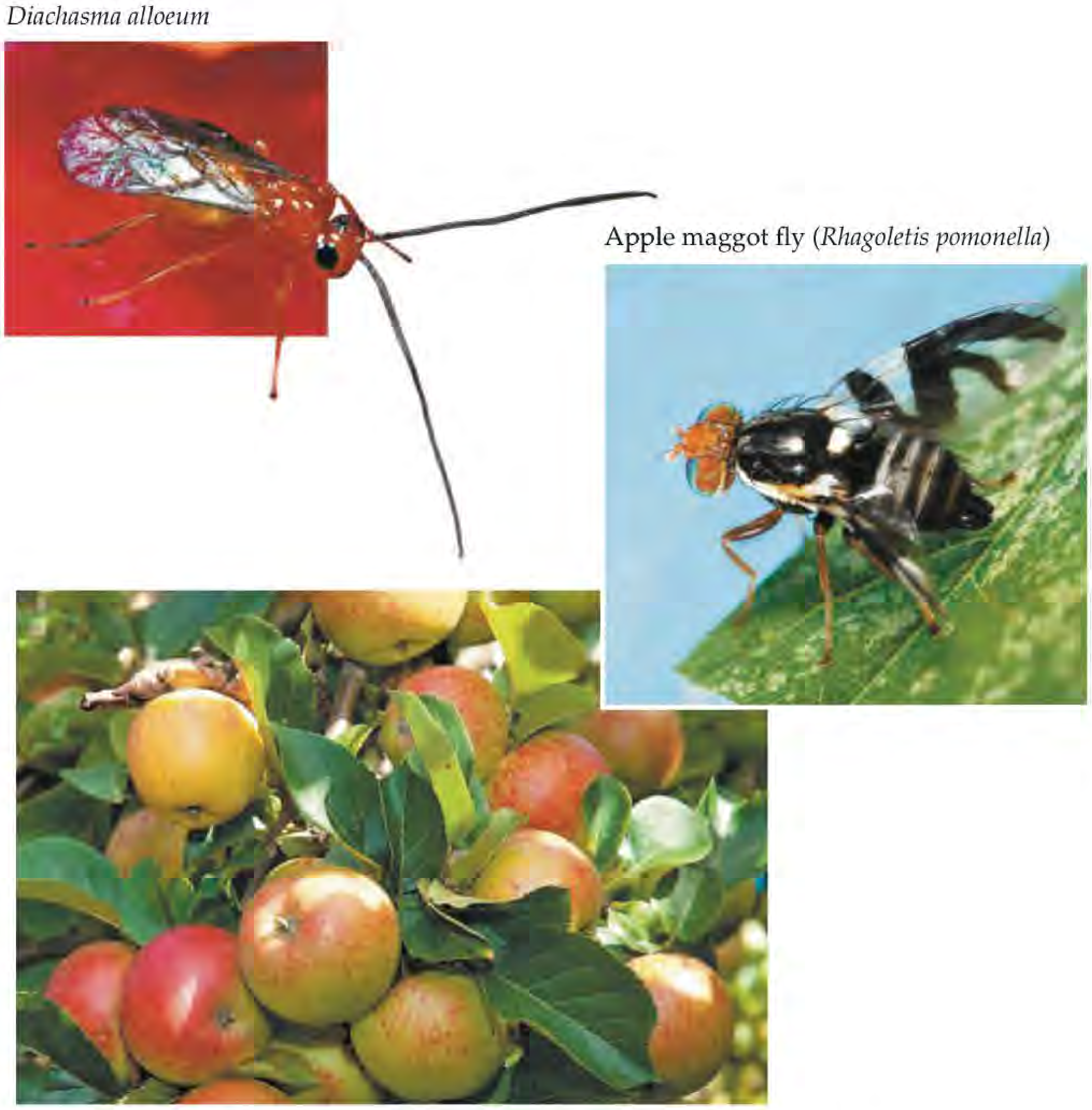


Figure 6.20 A Chain of Speciation Events Driven by Ecological Interactions? In the last 200 years, populations of the fly *Rhagoletis pomonella* that feed on apples have diverged genetically from their parent species, forming an incipient fly species. This change also appears to be leading to the formation of a new wasp species, *Diachasma alloeum*, that parasitizes members of apple-feeding *Rhagoletis* populations. (Photo of *D. alloeum* courtesy of Andrew Forbes.)

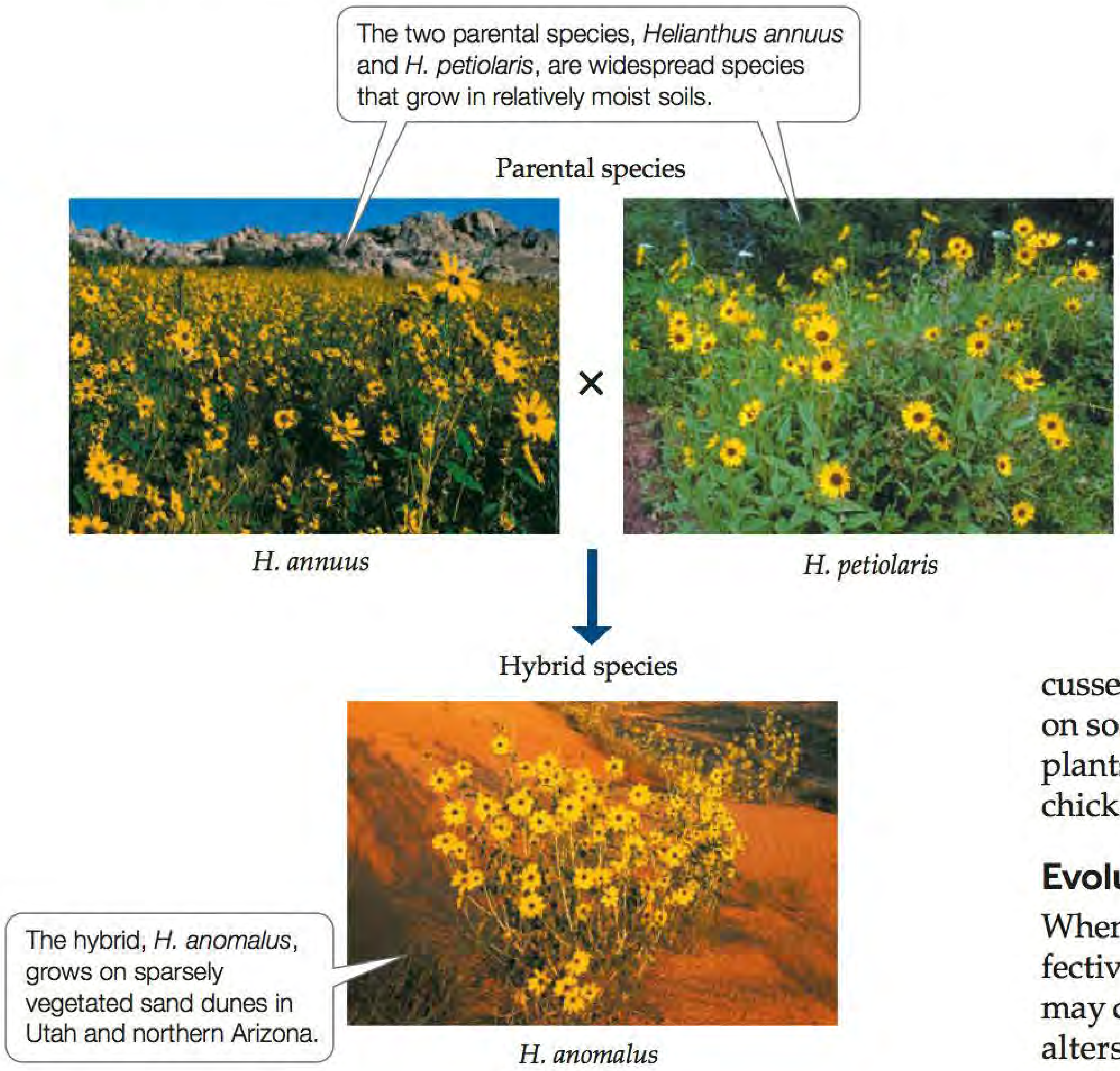
We turn next to a more detailed look at an idea that we have already encountered in this chapter: while ecological interactions influence evolution, evolution also influences ecological interactions.

CONCEPT 6.5

Ecological interactions and evolution exert a profound influence on one another.

Joint Effects of Ecology and Evolution

Ecological and evolutionary interactions can be so closely related as to be entangled. Consider the sunflower species *Helianthus anomalus*. This species originated from a speciation event in which two other sunflowers, *H. annuus* and *H. petiolaris*, produced hybrid offspring. As Loren Rieseberg and colleagues have shown in a series of experiments and genetic analyses (Rieseberg et al. 2003),



The two parental species, *Helianthus annuus* and *H. petiolaris*, are widespread species that grow in relatively moist soils.

The hybrid, *H. anomalus*, grows on sparsely vegetated sand dunes in Utah and northern Arizona.

Figure 6.21 A Hybrid That Lives in a New Environment The two sunflower species *Helianthus annuus* and *H. petiolaris* gave rise to a new hybrid species, *H. anomalus*. This species grows in a drier environment than either of the two parental species.

the new gene combinations generated by hybridization appear to have facilitated a major ecological shift in *H. anomalus*. This hybrid species grows in a much drier environment than does either of its two parental species (**Figure 6.21**)—an ecological shift that illustrates how evolution influences ecology. Simultaneously, however, life under different ecological conditions provided the selection pressures that molded the hybrid offspring of *H. annuus* and *H. petiolaris* into a new species, *H. anomalus*, showing how ecology influences evolution. Such joint ecological and evolutionary effects are common—as we should expect, given that both evolution and ecology depend on how organisms interact with one another and with their physical environment.

Ecological interactions can cause evolutionary change

Much of the drama of the natural world stems from the efforts of organisms to do three things: to eat, to avoid being eaten, and to reproduce. As organisms interact with one another in this drama, a web of ecological interactions results. These interactions can drive evolutionary change. We've already seen (in Concept 6.4) how predator–prey interactions caused long-term, large-scale, reciprocal evolution in which predators became more efficient at capturing prey and prey became more adept at escaping their predators. Predator–prey interactions are still causing evolutionary change today, as are a broad range of other ecological interactions, including herbivory, parasitism, competition, and mutualism (see Unit 4).

Studies of speciation have led to a similar conclusion: it is common for speciation to be caused by ecological factors (Schluter 1998; Funk et al. 2006). The effect of ecology on evolution is also clear from studies of relatively small evolutionary changes in populations. Examples discussed earlier in this chapter include directional selection on soapberry bugs caused by interactions with their food plants (see Figure 6.11) and genetic drift in greater prairie chickens caused by habitat loss (see Figure 6.8).

Evolution can alter ecological interactions

Whenever a group of organisms evolves a new, highly effective adaptation, the outcome of ecological interactions may change, and that change may have a ripple effect that alters the entire community. For example, if a predator evolves a new way of capturing prey, some prey species may be driven to extinction, while others may decrease in abundance, migrate to other areas, or evolve new ways to cope with the more efficient predator. Similar changes can occur among species that compete for resources; we will discuss one such example in Web Extension 14.2, in which evolutionary changes in experimental populations of one fly species reversed the outcome of its competitive interactions with another fly species.

Evolutionary changes that occur over long time scales also affect ecological interactions. For example, the origin and subsequent evolutionary diversification of plants altered the composition and stability of soils, the sources of food available to other organisms, and the cycling of nutrients—each of which had major effects on ecological interactions. By affecting soils, for example, early plants literally helped to build the habitats in which later communities of microorganisms, plants, and animals would eventually live and interact with one another.

Eco-evolutionary feedbacks can occur over short periods of time

As we discussed earlier in this chapter, evolution often occurs over short periods of time (e.g., months to decades). Because evolution occurs as organisms interact with each other and their physical environment, this suggests that reciprocal feedback effects between ecological and evolutionary factors also can occur over short periods of time. Let's take a closer look at the causes of these rapid feedback effects.

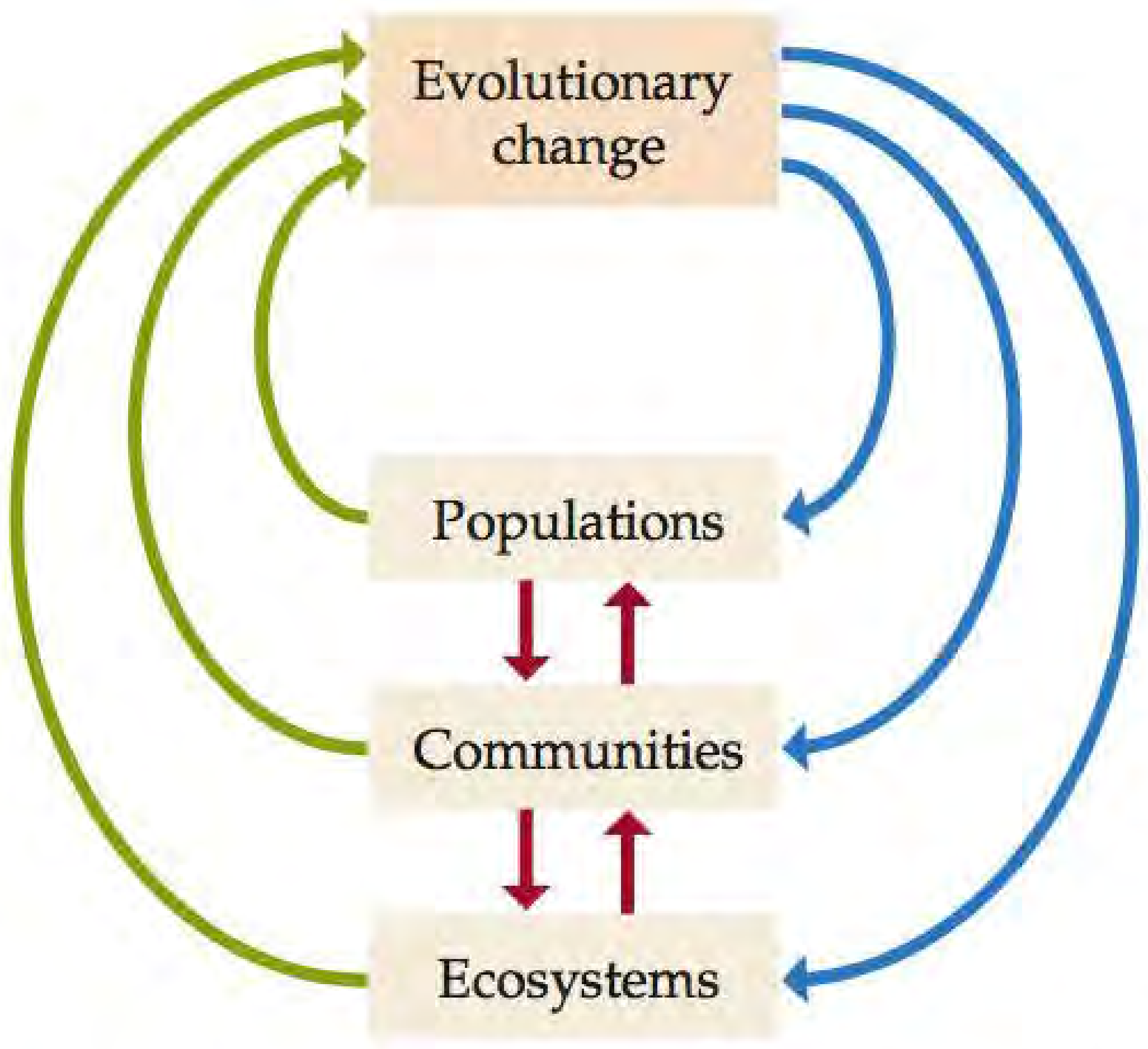


Figure 6.22 Rapid Feedback Effects Can Occur between Ecological and Evolutionary Factors Ecological change in a population, community, or ecosystem can drive evolutionary change over short periods of time (green arrows). Similarly, evolutionary change can alter events at the population, community, or ecosystem level (blue arrows). A change at one level of ecological organization can cause additional changes at other levels (red arrows), as when an increase in the population size of one species alters nutrient cycling in ecosystems.

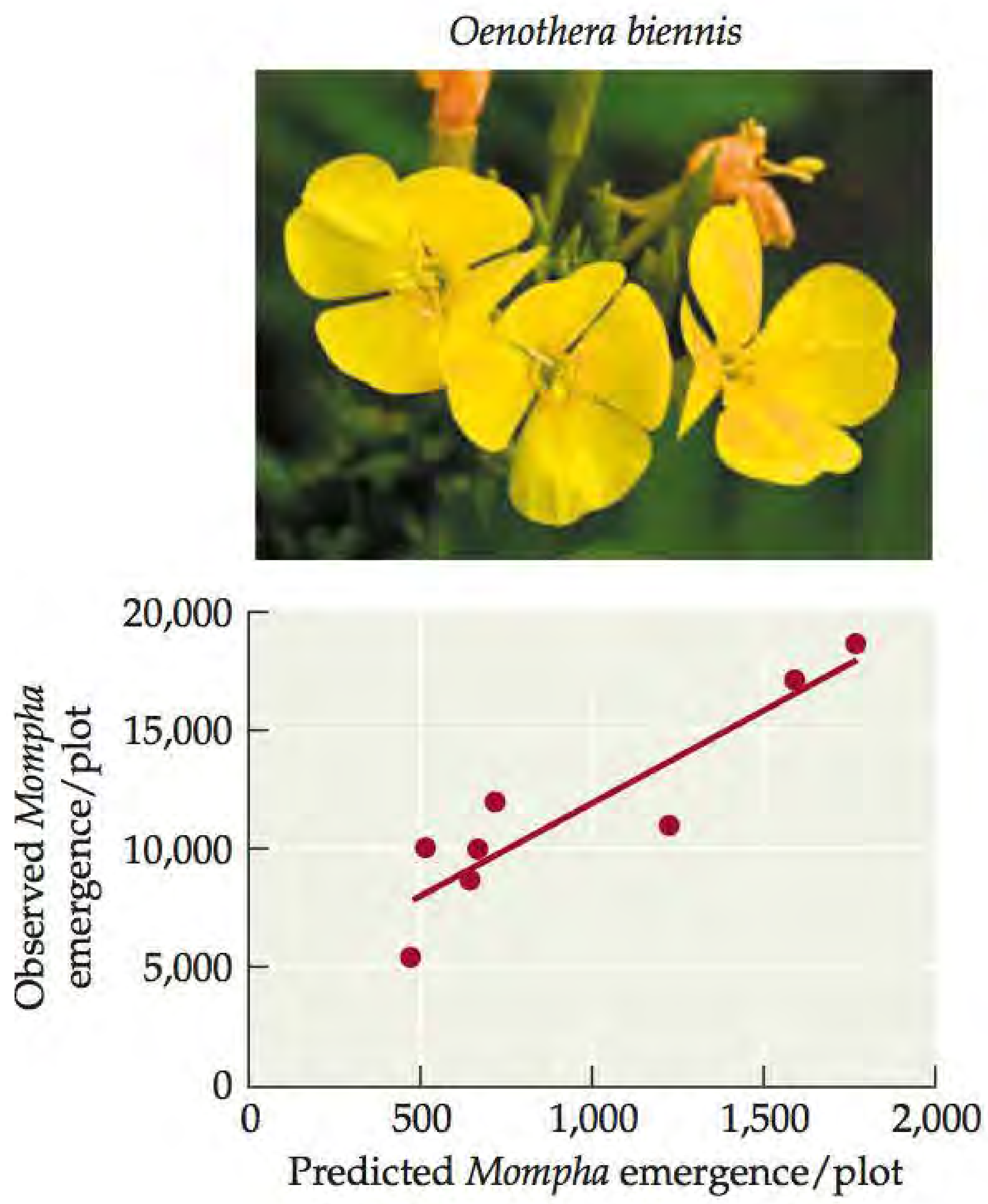


Figure 6.23 Feedback of Food Plant Evolution on Insect Abundance Caterpillars of the moth *Mompha brevivittella* eat the seeds of the evening primrose (*Oenothera biennis*). Some plant genotypes are more resistant to moth attack than others, indicating that moth abundance could change depending on plant genotype frequencies. In a 3-year field experiment, evolutionary changes in *O. biennis* genotype frequencies were correlated to moth abundance, indicating a feedback from evolution to ecology. (After Agrawal et al. 2013.)

? Suppose that eco-evolutionary feedbacks between changes in plant genotype frequency and moth abundance did not occur. Redraw this figure assuming that was the case.

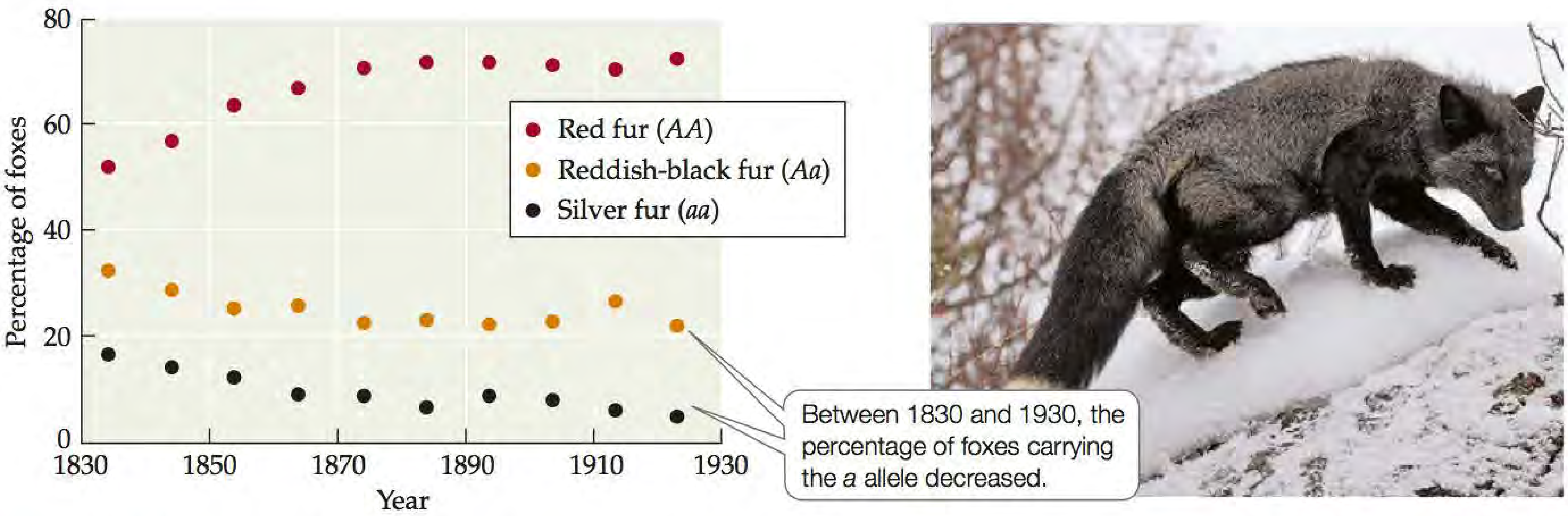
Feedback effects between ecological and evolutionary factors can occur when an ecological change, such as the addition or removal of a predator, alters the selective pressures that organisms face, thereby leading to evolutionary changes (**Figure 6.22**). Such evolutionary changes, in turn, can modify key aspects of populations, communities, or ecosystems. For example, in a 3-year field experiment (Agrawal et al. 2013), evolutionary changes in life span and flowering time in populations of the evening primrose (*Oenothera biennis*) led to consistent changes in the abundance of the moth *Mompha brevivittella*, which ate the seeds of this plant (**Figure 6.23**)—a demonstration that rapid evolution can cause rapid ecological change in a natural setting. Likewise, in the mountain streams of Trinidad, predator removal (an ecological change) leads to the evolution of larger body size in guppies over short periods of time, an evolutionary change that may increase the rate at which guppy populations add nitrogen to this freshwater ecosystem (El-Sabaawi et al. 2015). Overall, although the feedback effects shown in Figure 6.22 may be widespread, few studies have documented a full "reciprocity cycle" in nature in which an ecological change causes an evolutionary change that causes further ecological change (or vice versa).

A CASE STUDY REVISITED

Trophy Hunting and Inadvertent Evolution

Trophy hunters of bighorn sheep prefer to kill large males that carry a full curl of horns. The majority of these males are killed when they are between 4 and 6 years old, often before they have sired many offspring. As a result, hunting decreases the chance that alleles carried by males with a full curl of horns will be passed on to the next generation. Instead, it is males with relatively small horns who father most of the offspring, transmitting their alleles to the next generation. This change has caused the frequency of alleles encoding small horns to increase, thus leading to the observed 30-year decrease in average horn size (see Figure 6.2). Overall, trophy hunting has inadvertently caused directional selection in bighorn sheep, favoring small males with small horns and changing allele frequencies in the population over time.

Humans have caused unintended evolutionary changes in a wide variety of other populations. An early example was provided by the decline in the frequency of red foxes (*Vulpes fulva*) with coats that have a silver tint, a color preferred by hunters (**Figure 6.24**). In a medical example, shortly after antibiotics were first discovered (ca. 1940), their use was highly effective against bacteria that cause diseases and lethal infections. But the use of antibiotics provided a strong source of directional selection, leading to the evolution of antibiotic resistance in bacterial populations (see Figure 1.10). Today, as a result of this directional selection, antibiotic treatments sometimes fail,



Between 1830 and 1930, the percentage of foxes carrying the *a* allele decreased.

Figure 6.24 Hunting Resulted in the Decline of Silver Foxes Individual red foxes (*Vulpes fulva*) of genotype *AA* have red fur, and individuals of genotype *Aa* have reddish-black fur. Individuals of genotype *aa* are known as "silver foxes" because the tips of their hairs have a silver tint (photo). Hunters preferentially killed silver foxes because their furs yielded 2.5–4 times the price of other red fox furs. (After Elton 1942.)

? Based on the graph, estimate the initial (ca. 1832) and final (ca. 1923) frequencies of genotypes *AA*, *Aa*, and *aa*. Next, use the genotype frequencies that you estimated to compute the initial and final frequencies of the *a* allele. Hint: See footnote in Concept 6.1.

even when very high doses are administered. Antibiotic resistance also has enormous financial costs; in the United States alone, efforts to cure patients infected with antibiotic-resistant strains of just one bacterial species (*Staphylococcus aureus*) result in an estimated $24–$31 billion in medical expenses *each year* (Palumbi 2001).

We have seen throughout this chapter that human actions such as trophy hunting and antibiotic use act as selection pressures and hence may cause evolutionary change. But does our influence on evolution extend beyond cases in which we selectively kill other organisms?

CONNECTIONS IN NATURE

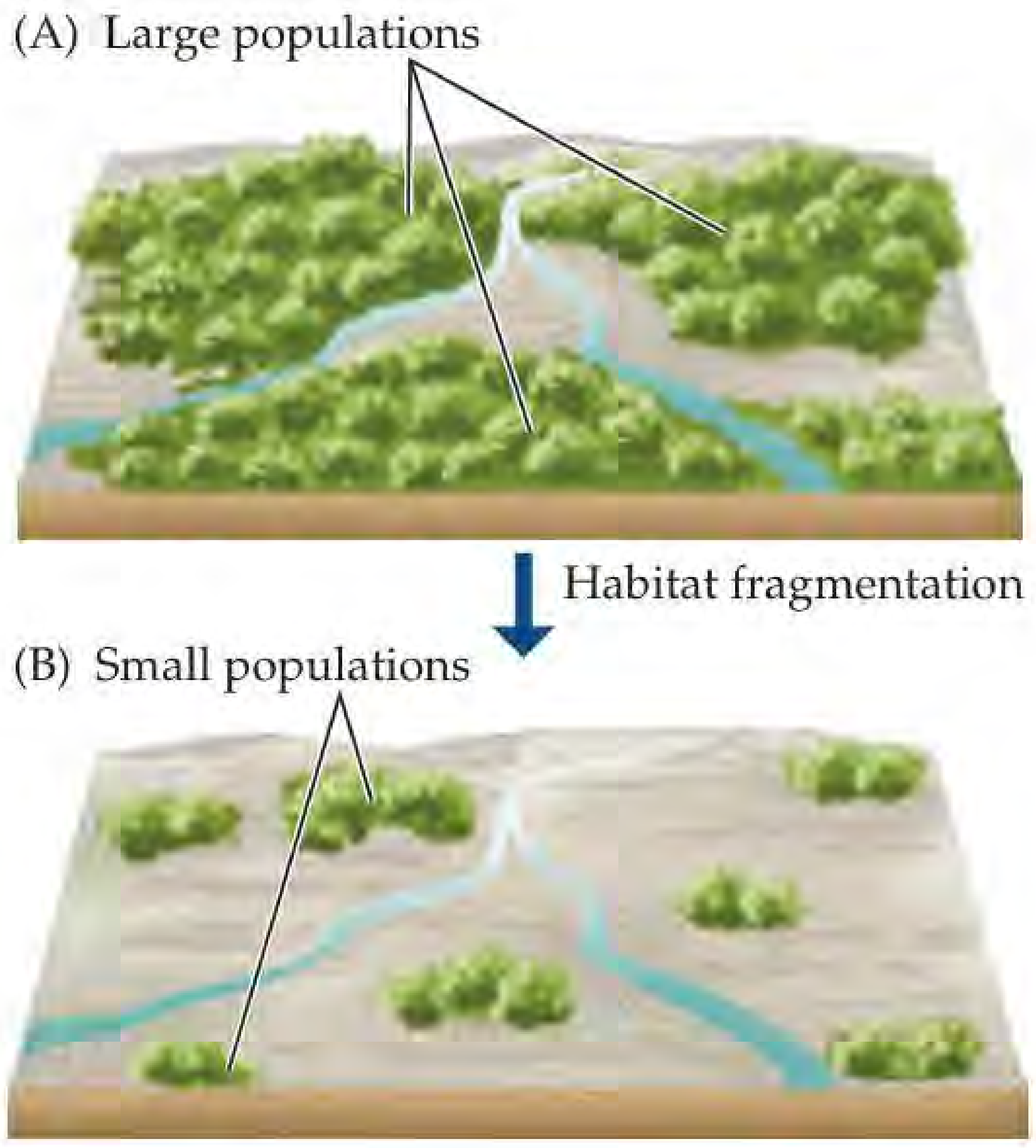
The Human Impact on Evolution

Many human actions alter the environment and hence have the potential to alter the course of evolution. As we've seen, actions such as trophy hunting, antibiotic use, and commercial fishing are themselves powerful sources of selection. Other human actions, such as emissions of pollutants or introductions of invasive species, change aspects of the abiotic or biotic environment. By changing features of the environment, these and many other human actions can cause evolutionary change. In **Analyzing Data 6.1**, you'll analyze data related to a classic example of this process, in which the emission (and subsequent control) of pollutants caused evolution by natural selection in populations of the peppered moth (*Biston betularia*).

Still other human actions, such as *habitat fragmentation* (in which portions of a species' habitat are destroyed, leaving spatially isolated fragments of the original habitat), can also cause large evolutionary changes (**Figure 6.25**). In general, human actions that affect the environment can alter each of the three main mechanisms of evolution: natural selection, genetic drift, and gene flow. Because we know with certainty that our actions are causing great changes to environments worldwide, we can infer that they are also causing evolutionary changes in populations worldwide.

As another example of human-caused evolution, consider the effects of adding nutrients such as nitrogen from sewage and fertilizers to lakes. Such nutrient inputs can cause the clarity and oxygen concentration of the water to drop (see Concept 22.4), leading to unintended evolutionary effects. For example, nutrient inputs to European lakes have reduced the effectiveness of reproductive barriers that once isolated species of whitefish (Vonlanthen et al. 2012). Murky (low-clarity) waters can hinder the ability of females to recognize males of their own species, thus making it more likely that a female will select a male from another whitefish species as her mate. When interspecific mating is common, a "speciation reversal" can occur in which two previously isolated species fuse into a single, hybrid species. Vonlanthen et al. concluded that nutrient inputs have caused such speciation reversals, leading to the extinction of eight whitefish species. As we'll see in later chapters of this book, such reductions in the diversity of species can have wide-ranging ecological effects.

Human actions also have the potential to alter patterns of evolution over long time scales. For example, the extinction rate of species today is 100 to 1,000 times higher than the usual, or background, extinction rate seen in the fossil record for times when no mass extinction was taking place. Human actions such as habitat destruction, overharvesting, and introductions of invasive species are among the main reasons for this rise in the extinction rate (see Concepts 23.3 and 24.2). Extinction is forever, so when human actions drive a species to extinction, the future course of evolution is altered in a way that cannot be reversed. If human activities cause a sixth mass extinction in the next few centuries or millennia, our actions will greatly and irreversibly change the evolutionary history of life on Earth.



	UNFRAGMENTED HABITAT	FRAGMENTED HABITAT
Population size	Large	Small
Distance between populations	Short	Long
Genetic drift	Low impact	High impact
Genetic variation within populations	High	Low
Gene flow	High	Low

Figure 6.25 Evolutionary Effects of Habitat Fragmentation on a Hypothetical Species (A) Prior to habitat fragmentation, there are many individuals in each population of the species, and the distances between populations are short. (B) When human activities remove large portions of the habitat, the population sizes shrink, and the distances between populations increase, causing evolutionary changes that decrease the potential for adaptive evolution of the species and increase its risk of extinction.

ANALYZING DATA 6.1 Does Predation by Birds Cause Evolution in Moth Populations?

YEAR	NO. OF LIGHT MOTHS RELEASED	NO. OF DARK MOTHS RELEASED	NO. OF LIGHT MOTHS EATEN	NO. OF DARK MOTHS EATEN
2002	706	101	162	31
2003	731	82	204	24
2004	751	53	128	17
2005	763	58	166	18
2006	774	34	145	6
2007	797	14	158	4

The peppered moth (*Biston betularia*) has a light-colored and a dark-colored form. The first dark-colored moth was observed in 1848 near Manchester, England; 50 years later, most moths in the area were dark in color. Researchers hypothesized that dark-colored moths increased in frequency because when the moths rested on trees whose bark had been darkened by pollution, it was harder for predators to find dark moths than light moths. In particular, field studies by Kettlewell (1955, 1956) indicated that natural selection by birds favored dark-colored moths in regions where tree bark was blackened by pollution, whereas light-colored moths were favored elsewhere.

After clean air legislation was enacted in England in 1956, tree surfaces lightened over time because of the reduction in soot and the growth of lichens on the trees' bark (lichens are light in color, and they grow poorly in polluted air). During this period, the dark-colored moths decreased in frequency, as shown for the region around Manchester in **Web Extension 6.3**.

Although the rise and fall in the frequency of dark-colored moths were consistent with typical results from natural selection by bird predation, criticisms have been leveled against aspects of this hypothesis. For example, abnormally high densities of moths were released in some experiments, potentially increasing the impact of predation, because some predators preferentially attack abundant prey. Over the course of a 6-year experiment designed to address such criticisms, Michael Majerus released thousands of moths in an area where tree surfaces had been lightened. He determined the number of light- and dark-colored moths that were eaten. His results are reported in the table (data from Cook et al. 2012).*

1. The densities (and proportions) of the light- and dark-colored moths that Majerus released were similar to those he observed in the field. Why is this important to the validity of the experiment?
2. Use the proportions of dark moths that Majerus released to determine whether dark-colored moths were increasing or decreasing in frequency in the area where he conducted the experiment (Cambridge, England).
3. Calculate the percentages of released dark- and light-colored moths that were eaten each year, and graph those percentages versus time. Do the results support the hypothesis that evolution by natural selection caused the frequency of dark-colored moths to change over time? Explain.

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*Cook, L. M., B. S. Grant, I. J. Saccheri and J. Mallet. 2012. Selective bird predation on the peppered moth: The last experiment of Michael Majerus. *Biological Letters* 8: 609–612.

See the companion website for a similar ANALYZING DATA exercise.

Summary

CONCEPT 6.1 Evolution can be viewed as genetic change over time or as a process of descent with modification.

- Biologists often define evolution in a relatively narrow sense as change over time in the frequencies of alleles in a population.
- Evolution can also be viewed as descent with modification, a process in which populations accumulate differences over time and hence differ from their ancestors.
- Natural selection modifies populations by favoring individuals with some heritable traits over other individuals.
- Although natural selection acts on individuals, an individual does not evolve—either it has a favored trait or it does not. Only populations evolve.

CONCEPT 6.2 Natural selection, genetic drift, and gene flow can cause allele frequencies in a population to change over time.

- Mutation and recombination are the sources of new alleles and new combinations of alleles, thereby providing the genetic variation on which evolution depends.
- wNatural selection occurs when individuals with certain heritable phenotypic traits survive and reproduce more successfully than individuals with other traits.
- Genetic drift, which occurs when chance events determine which alleles are passed from one generation to the next, can have negative effects on small populations.
- Gene flow, the transfer of alleles between populations, makes populations more similar to one another genetically and can introduce new alleles into populations.

CONCEPT 6.3 Natural selection is the only evolutionary mechanism that consistently causes adaptive evolution.

- By consistently favoring individuals that have advantageous alleles over individuals that have other alleles, natural selection can cause adaptive evolution, in which the frequency of an advantageous trait in a population increases over time.
- Natural selection can increase the frequency of advantageous traits rapidly—in days to years, depending on the organism and the selection pressure.
- Gene flow can limit the extent to which a population is adapted to its local environment.
- Constraints on adaptive evolution result from factors such as lack of genetic variation, evolutionary history, and ecological trade-offs.

CONCEPT 6.4 Long-term patterns of evolution are shaped by large-scale processes such as speciation, mass extinction, and adaptive radiation.

- The genetic divergence of populations over time can lead to speciation, the process by which one species splits into two or more species. Speciation requires the evolution of reproductive barriers between populations.
- The number of species in a group of organisms increases when more species are produced by speciation than are lost to extinction, and decreases when the reverse is true. The outcome of this process can be visualized with an evolutionary tree.
- Biological communities can lose much of their diversity in mass extinctions, global events in which large proportions of Earth's species are driven to extinction in a relatively short time.
- An adaptive radiation occurs when a group of organisms gives rise to many new species that expand into new habitat or fill new ecological roles.
- Adaptive radiations can be promoted by factors such as the removal of competitor groups by a mass extinction or the evolution of a major new adaptation.

CONCEPT 6.5 Ecological interactions and evolution exert a profound influence on one another.

- Ecological interactions among organisms and between organisms and their environment can cause evolutionary changes, ranging from allele frequency changes in populations to the formation of new species.
- Similarly, evolutionary change can alter the outcomes of ecological interactions, thus having a large influence on biological communities.

Review Questions

1. Natural selection acts on individuals, yet one of the points made in this chapter is that *populations evolve, but individuals do not*. Explain how natural selection works and why the italicized statement is true.
2. What causes adaptive evolution? Explain in your answer why each of the three primary mechanisms of allele frequency change in populations causes or does not cause adaptive evolution.
3. What large-scale processes determine patterns of evolution observed over long time scales? Explain how each process that you describe has this effect.
4. Explain why ecological interactions and evolutionary change have joint effects, each affecting the other.
5. More than 100 years ago, Rutter (1902) expressed concern about the effects of fishing on river salmon. He wrote (p. 134), "A large fish is worth more on the market than a small fish; but so are large cattle worth more on the market than small cattle, yet a stock raiser would never think of selling his fine cattle and keeping only the runts to breed." From an evolutionary perspective, summarize the reasons for Rutter's concern, and describe how harvesting-induced evolution is thought to affect fish populations today.

Hone Your Problem-Solving Skills

Stuart and colleagues (2014) studied how the invasion of islands in Florida by the Cuban brown anole lizard (*Anolis sagrei*) affected the native anole, *A. carolinensis*. After *A. sagrei* invaded, *A. carolinensis* moved to higher tree perches. Stuart and colleagues tested whether this change in habitat use caused evolution in the *A. carolinensis* toepad area; a larger toepad area improves the ability of lizards to grasp the slender branches found high in trees. They measured the toepad area of *A. carolinensis* caught in the wild on islands that were uninvaded and on islands invaded by *A. sagrei*. They also measured *A. carolinensis* toepad area in a "common garden experiment" in which *A. carolinensis* eggs collected on uninvaded and on invaded islands were reared to adulthood under identical conditions. Average toepad areas are shown in the table.

	WILD CAUGHT		COMMON GARDEN	
	UNINVADED ISLANDS	INVADED ISLANDS	UNINVADED ISLANDS	INVADED ISLANDS
Toepad area (size-corrected index)	1.04	2.55	0.96	2.21

1. Make a bar graph (see the **Web Stats Review**, section 1.1.2) of results for wild-caught and common garden *A. carolinensis*. Compare the results for uninvaded versus invaded islands.
2. When traits such as toepad area differ consistently between lizards living on uninvaded versus invaded islands, those differences may be due to evolution, phenotypic plasticity,* or both. Suppose that evolution had been the primary cause of differences in toepad area between lizards from uninvaded versus invaded islands. Under that assumption, predict whether wild-caught results would differ from common garden results. Explain.
3. Suppose that phenotypic plasticity had been the primary cause of differences in toepad area between lizards from uninvaded versus invaded islands. Under that assumption, predict whether wild-caught results would differ from common garden results. Explain.
4. Did the invasion of Florida islands by *A. sagrei* lead to eco-evolutionary effects? Explain.

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* Phenotypic plasticity refers to nonheritable phenotypic variation that occurs when individuals have different phenotypes depending on environmental conditions experienced during their lifetime. For example, plants may be taller or produce more seeds if they have ample nutrients than if they do not, while people may have larger muscles if they lift weights regularly than if they do not.

ON THE COMPANION WEBSITE

ecology4e.sinauer.com

The website includes companions to all of the Analyzing Data exercises, Online Quizzes, Flashcards, Suggested Readings, and more. In addition, the following resources are available for this chapter:

Hands-On Problem Solving

6.1 Down the River of Life: Natural Selection and Genetic Drift

Web Extensions

6.1 Hardy–Weinberg Equation

6.2 Evolutionary Responses to Global Warming in *Drosophila subobscura*

6.3 Selection against Dark-Colored Forms of the Peppered Moth, *Biston betularia*

Online Climate Change Connection

6.1 Evolution and Climate Change

7

Life History

KEY CONCEPTS

CONCEPT 7.1 Life history patterns vary within and among species.

CONCEPT 7.2 Reproductive patterns can be classified along several continua.

CONCEPT 7.3 There are trade-offs between life history traits.

CONCEPT 7.4 Organisms face different selection pressures at different life cycle stages.

Nemo Grows Up: A Case Study

Birds do it, bees do it, even educated fleas do it—they all produce offspring that perpetuate their species. But beyond that basic fact of life, the offspring produced by different organisms vary tremendously. A grass plant produces seeds a few millimeters long that can wait, buried in the soil, for years until conditions are right for germination. A sea star spews hundreds of thousands of microscopic eggs that develop adrift in the ocean. A rhinoceros produces one calf that develops in her womb for 16–18 months and can walk well several days after birth, but requires more than a year of care before it becomes fully independent (**Figure 7.1**).

Even this broad range of possibilities barely begins to describe the different ways in which organisms reproduce. In popular media, we humans often depict other animals as having family lives similar to ours. For example, in the animated film *Finding Nemo*, clownfish live in families with a mother, a father, and several young offspring. When Nemo the clownfish loses his mother to a predator, his father takes over the duties of raising him. But in a more realistic version of this story, after losing his mate, Nemo's father would have done something less predictable: he would have changed sex and become a female.

Actually, the correspondence between the movie and biology breaks down long before Nemo loses his mother. Clownfish spend their entire adult lives within a single sea anemone (**Figure 7.2**). Anemones can be thought of as modified upside-down jellyfish with a central mouth ringed by stinging tentacles. In what appears to be a mutually beneficial relationship, the anemone protects the clownfish by stinging their predators, but the clownfish themselves are not stung. The clownfish, in turn, may help the anemone by eating its parasites or driving away its predators.

Two to six clownfish typically inhabit a single anemone, but they are far from a traditional human family—in fact, they are usually not related to one another. The clownfish that live in an anemone interact according to a strict pecking order that is based on size. The largest fish in the anemone is a female. The next fish in the hierarchy, the second largest, is the breeding male. The remaining fish are sexually immature *nonbreeders*. If the female dies, as in Nemo's story, the breeding male undergoes a growth spurt and changes sex to become a female, and the largest nonbreeder increases in size and becomes the new breeding male.

The breeding male clownfish mates with the female and cares for the fertilized eggs until they hatch. The hatchling fish leave the anemone to live in the open ocean, away from the predator-infested reef. The young fish eventually return to the reef and develop into juveniles. Then they

Figure 7.1 Offspring Vary Greatly in Size and Number Organisms produce a large range of offspring numbers and sizes. A rhinoceros produces a single calf that weighs 40–65 kg (90–140 pounds). On the other end of the spectrum, many plants produce hundreds to thousands of seeds that are less than a millimeter long and weigh as little as 0.8 μg (roughly one fifty-billionth the weight of a rhinoceros calf).

Figure 7.2 Life in a Sea Anemone Clownfish (*Amphiprion percula*) form hierarchical groups of unrelated individuals that live and reproduce among the tentacles of their anemone host (*Heteractis magnifica*).

Predict the gender of each of these clownfish (assuming that they live together as a group of four fish in an anemone host). Explain your answer.

must find an anemone to inhabit. When a juvenile fish enters an anemone, the resident fish allow it to stay there only if there is room. If there is no room, the young fish is expelled and returns to the dangers of an exposed existence on the reef.

This life cycle, with its expulsions, hierarchies, and sex changes, is certainly as colorful as the fish that live it. But why do clownfish engage in these complicated machinations just to produce more clownfish? Organisms have arrived at a vast array of solutions to the basic problem of reproduction. As we will see, these solutions are often well suited for meeting the challenges and constraints of the environment where a species lives.

Introduction

Human history is a record of past events. Your personal history might consist of a series of details about the course of your life: your birth weight, when you started walking and talking, your adult height, and other relevant information about your development. Similarly, an individual organism's **life history** consists of major events related to its growth, development, reproduction, and survival.

In this chapter, we'll discuss traits that characterize the life history of an organism, including age and size at sexual maturity, amount and timing of reproduction, and survival and mortality rates. As we'll see, the timing and nature of life history traits, and therefore the life history itself, are products of adaptation to the environment in which the organism lives. We'll also consider how biologists analyze life history patterns in order to understand the tradeoffs, constraints, and selection pressures imposed on different stages of an organism's life cycle.

CONCEPT 7.1
Life history patterns vary within and among species.

Life History Diversity

The study of life histories is concerned with categorizing variation in life history traits and analyzing the causes of that variation. In order to understand such analyses, it is helpful first to examine some of the broad life history patterns found within and among species.

Individuals within species differ in their life histories

Individual differences in life history traits are ubiquitous. Think about your own life experiences and those of your family and friends. Some members of your social group reached developmental milestones such as puberty earlier or later than others. Different women may have different numbers of children with different age gaps between them. Despite this variation, it is possible to make some generalizations about life histories in *Homo sapiens*: for example, women typically have one baby at a time, reproduction usually occurs between the ages of 15 and 45, and so on. Similar generalizations can be made for other species. The **life history strategy** of a species is the overall pattern in the timing and nature of life history events averaged across all the individuals in the species (**Figure 7.3**).

The life history strategy is shaped by the way the organism divides its energy and resources between growth, reproduction, and survival. Within a species, individuals often differ in how they divide their energy and resources among these activities. Such differences may result from genetic variation, from differences in environmental conditions, or from a combination of both.

GENETIC DIFFERENCES Some life history variation within species is determined genetically. Genetically influenced traits can often be recognized as those that are more similar within families than between them. Again, these kinds of traits are familiar in humans: for example, siblings are often similar in appearance and reach similar adult heights and weights. The same is true in other organisms. For example, in bluegrass (*Poa annua*), life history

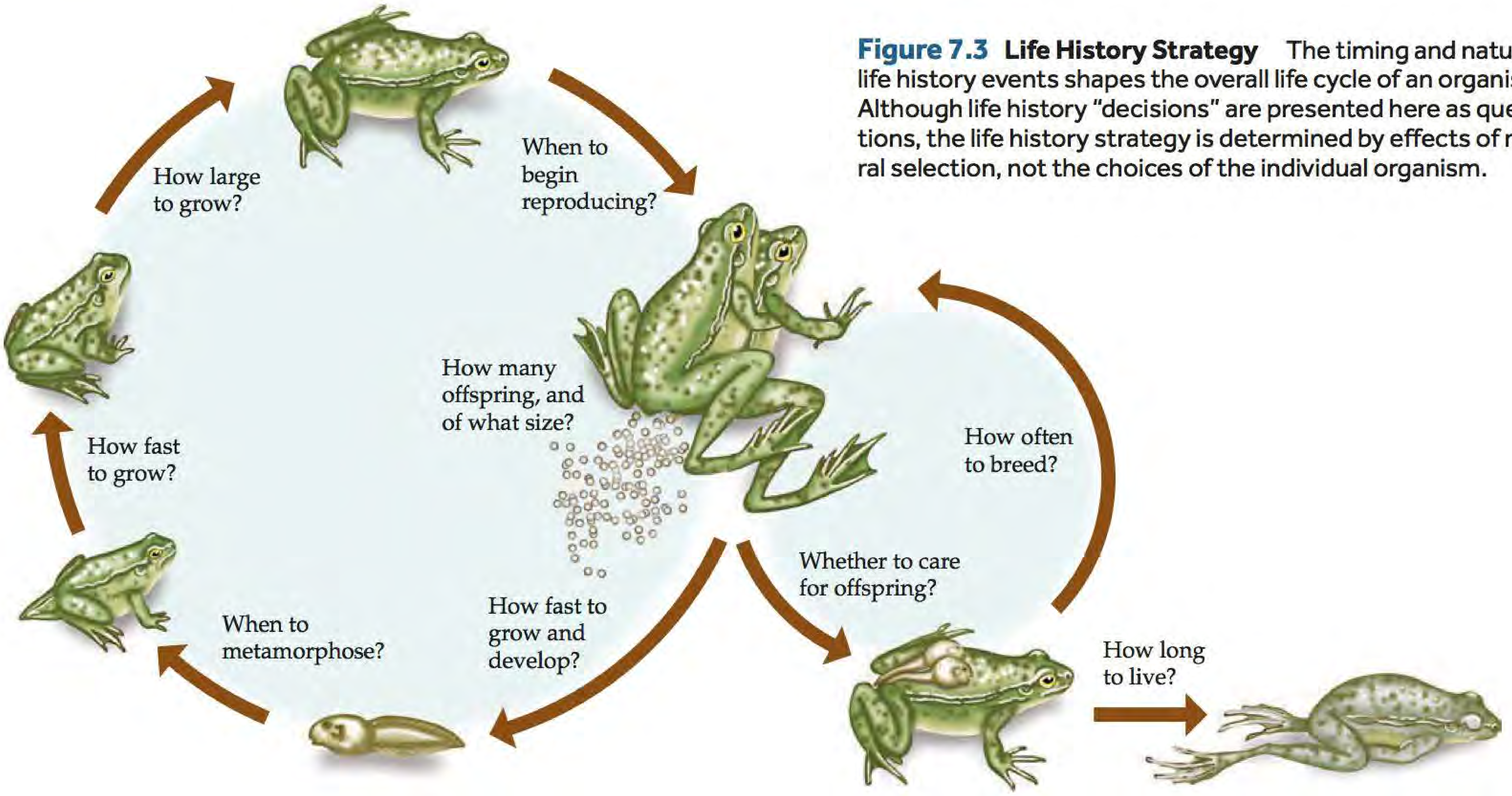


Figure 7.3 Life History Strategy The timing and nature of life history events shapes the overall life cycle of an organism. Although life history "decisions" are presented here as questions, the life history strategy is determined by effects of natural selection, not the choices of the individual organism.

traits such as age at first reproduction, growth rate, and number of flowers produced are similar among sibling plants (Law et al. 1977). As with any other trait, heritable variation in life history traits is the raw material on which natural selection acts. Selection favors individuals whose life history traits result in their having a better chance of surviving and reproducing than do individuals with other life history traits.

Much of life history analysis is concerned with explaining how and why life history patterns have evolved to their present states. Ecologists sometimes describe life histories as *optimal* in that they are adapted to maximize **fitness** (the genetic contribution of an organism's descendants to future generations). However, no organism has a perfect life history—that is, one that results in the unlimited production of descendants. Instead, all organisms face *constraints* that prevent the evolution of a perfect life history. As we'll see in Concept 7.3, these constraints often involve ecological trade-offs in which an increase in the performance of one function (such as reproduction) can reduce the performance of another (such as growth or survival). Thus, although life histories often serve organisms well in the environments in which they have evolved, they are optimal only in the sense of maximizing fitness subject to constraints.

ENVIRONMENTAL DIFFERENCES A single genotype may produce different phenotypes under different environmental conditions, a phenomenon known as **phenotypic plasticity**. Almost every trait shows some degree of plasticity, and life history traits are no exception. For example, most plants and animals grow at different rates depending on temperature. They do so because development typically speeds up as the temperature rises, then slows down again due to heat stress as the temperature approaches the organism's upper lethal temperature.

Changes in life history traits often translate into changes in adult morphology. Slower growth under cooler conditions, for example, may lead to a smaller adult size or to differences in adult shape. Callaway and colleagues (1994) showed that ponderosa pine (*Pinus ponderosa*) trees grown in cool, moist climates allocate more biomass to leaf growth relative to sapwood production than do those in warmer desert climates ("sapwood" refers to newly formed layers of wood that function in water transport). **Allocation** describes the relative amounts of energy or resources that an organism devotes to different functions. The result of allocation differences in ponderosa pines is that trees grown in different environments differ in adult shape and size. Desert trees are shorter and squatter, with fewer branches and leaves (**Figure 7.4**). As a result of having fewer leaves, they also lose less water, have lower photosynthetic rates, and consume less CO_2.

Phenotypic plasticity that responds to temperature variation often produces a continuous range of sizes. In other types of phenotypic plasticity, a single genotype produces discrete types, or **morphs**, with few or no intermediate forms. For example, populations of spadefoot toad (*Spea multiplicata*) tadpoles in Arizona ponds contain two morphs: omnivore morphs, which feed on detritus and algae, and larger carnivore morphs, which feed on fairy shrimp and on other tadpoles (**Figure 7.5**). The

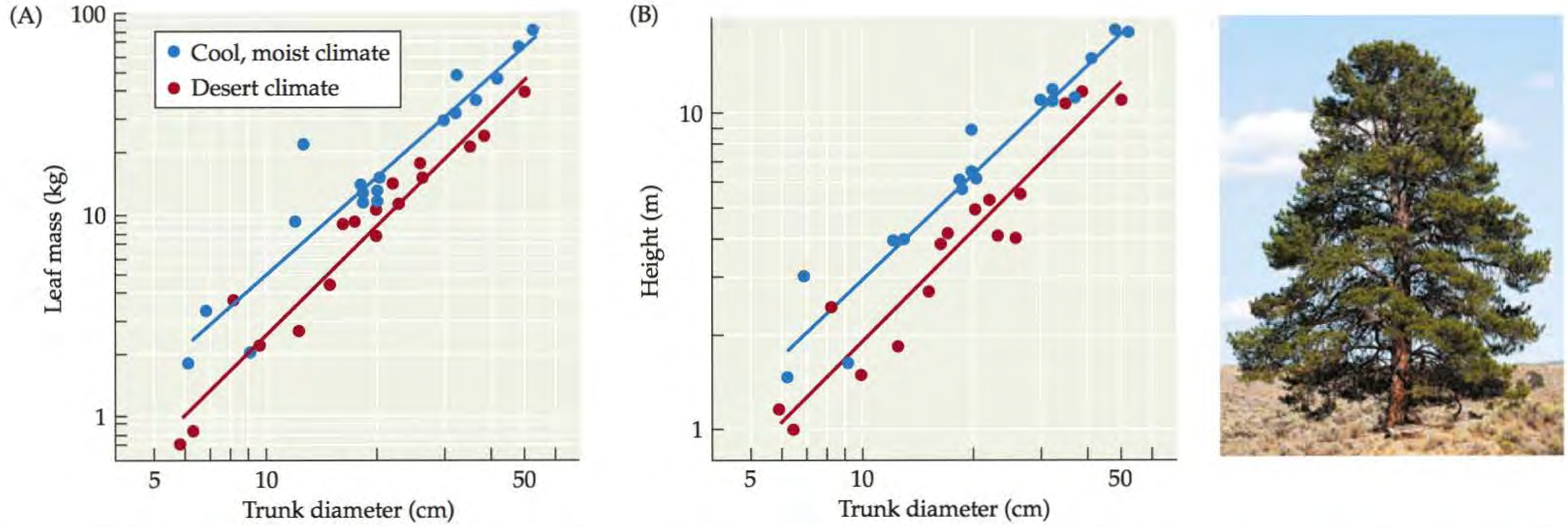


Figure 7.4 **Plasticity of Growth Form in Ponderosa Pines** (A) Ponderosa pine trees (*Pinus ponderosa*) in cool, moist climates allocate more resources to leaf production than do trees in desert climates. (B) Desert trees are shorter than those grown in cooler climates, but for a given height, they have thicker trunks. (After Callaway et al. 1994.)

? Use the solid (regression) lines in (B) to estimate the trunk diameter of a tree that is 5 m tall and grows in a cool, moist climate versus the trunk diameter of a tree of the same height that grows in a desert climate.

differing body shapes of omnivores and carnivores result from differences in the relative growth rates of different body parts: carnivores have bigger mouths and stronger jaw muscles because of accelerated growth in those areas. Pfennig (1992) showed that omnivore tadpoles can turn into carnivores when fed on shrimp and tadpoles, and field studies show that the proportion of omnivore and carnivore morphs is affected by food supply. Carnivore tadpoles grow faster and are more likely to metamorphose before the ponds where they live dry up; thus, the rapidly growing carnivores are favored in ephemeral ponds. The more slowly growing omnivores are favored in ponds that persist longer, because they metamorphose in better condition and thus have better chances of survival as juvenile toads.

When thinking about examples such as the omnivore and carnivore morphs of the spadefoot toad, it is tempting to assume that phenotypic plasticity is adaptive—that the ability to produce different phenotypes in response to changing environmental conditions increases the fitness of individuals. While that is often the case, adaptation must be demonstrated rather than assumed. For example, it may be adaptive for ponderosa pines to be stockier and have fewer leaves in hot, dry climates because these features can help reduce water loss. However, adaptation would have to be documented by measuring and comparing the survival and reproductive rates of stockier and taller trees in the desert environment. In some instances, phenotypic plasticity may be a simple physiological response, not an adaptive response shaped by natural selection. For example, as mentioned above, growth rate typically increases with temperature up to a point. This may occur because

Omnivores feed on the pond bottom on detritus.

Carnivores feed in the water column on fairy shrimp.

Figure 7.5 **Phenotypic Plasticity in Spadefoot Toad Tadpoles** Spadefoot toad (*Spea multiplicata*) tadpoles can develop into small-headed omnivores (A) or large-headed carnivores (B), depending on the food they consume early in development. Later in development, o mnivores and carnivores feed on different food sources that are located in different portions of their habitat. (Courtesy of David Pfennig.)

chemical reactions are slower at lower temperatures, and thus metabolism and growth are necessarily slower.

CLIMATE CHANGE CONNECTION

Climate Change and the Timing of Seasonal Activities

The timing of seasonal life history activities can be of critical importance. For example, a bird that migrates north too early in the spring may starve if no food is available, while a plant that flowers when its pollinators are not present may fail to reproduce. As described in Concept 4.2, the timing of such seasonal events is affected by changing day length (photoperiod) and sometimes by other environmental cues such as temperature that also vary over the course of a year. As the climate has changed in recent decades, have species adjusted the times when they perform key seasonal activities?

Long-term data sets show that many species are initiating spring activities earlier than they once did, apparently in response to climate change. For example, as the climate warms, leaf production in plants, egg laying in birds, emergence from dormancy in insects, and arrival of migratory animals often occur earlier today than they did in the 1960s and 1970s.

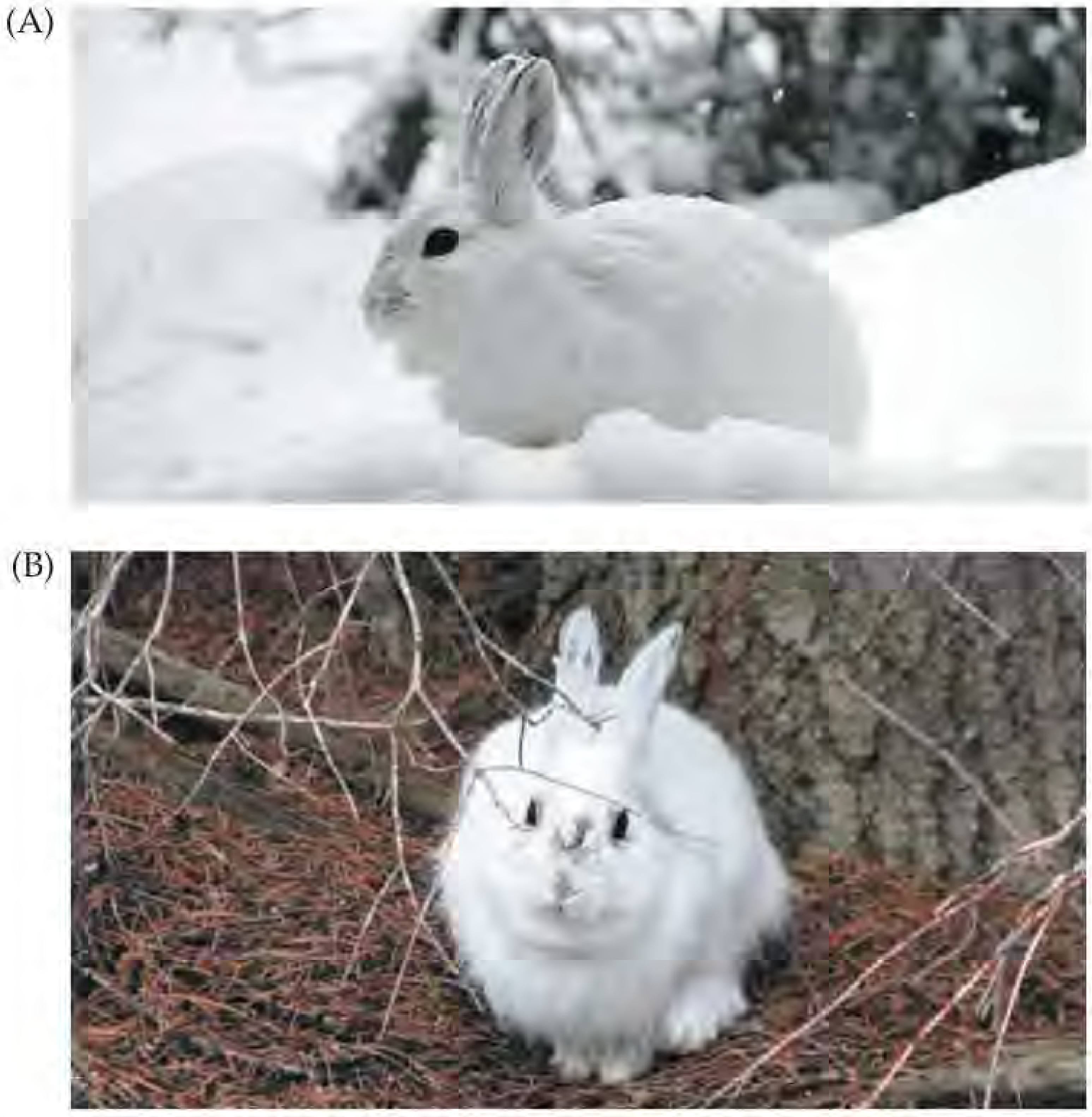


Figure 7.6 Camouflage Mismatch in Snowshoe Hares (A) Historically, snowshoe hares changed their color from brown to white at a time of year that matched the onset of snowfall, causing them to be well-camouflaged all winter. (B) With climate warming, snowfall now begins later in the year. However, the date of the fall coat-color change has remained the same, causing an increase in the number of days that snowshoe hares experience a camouflage mismatch. (A from Mills et al. 2013; B courtesy of Scott Mills.)

In some cases, however, shifts in the timing of seasonal activities have not kept pace with climate change. Consider the snowshoe hare (*Lepus americanus*). As winter approaches, the coat color of snowshoe hares changes from brown to white, providing camouflage against snow; the reverse coat-color change occurs in spring. As the climate has warmed, the length of time that the ground is covered by snow has decreased because snowfall now begins later in autumn and snowmelt occurs earlier in spring. If the timing of the fall coat-color change in snowshoe hares had kept pace with the delay in when snowfall begins, we would expect that snowshoe hares would molt to white later in the fall than they once did. Instead, however, the date and rate of the fall molt has not changed (Mills et al. 2013). As a result, the number of days in which a "camouflage mismatch" occurs has increased, making the hares easier for visually hunting predators to spot (**Figure 7.6**) and leading to increased mortality rates (Zimova et al. 2016). Mismatches in the timing of seasonal activities have also been found in caribou (*Rangifer tarandus*) and snow geese (*Chen caerulescens*): although the plants their young require for food are producing leaves earlier in the spring, neither species has adjusted the timing of reproduction. This has caused a decline in the reproductive success of both species because their young are not getting enough to eat.

Mode of reproduction is a basic life history trait

At the most basic level, evolutionary success is determined by successful reproduction. Despite this universal reality, organisms have evolved vastly different mechanisms for reproducing—from simple asexual splitting to complex mating rituals and intricate pollination systems.

ASEXUAL REPRODUCTION The first organisms to evolve on Earth reproduced asexually by *binary fission* ("dividing in half"). The sexual reproductive processes of meiosis, recombination, and fertilization arose later. Today, all prokaryotes and many protists reproduce asexually. While sexual reproduction is the norm in multicellular organisms, many can also reproduce asexually. For example, after they are initiated by a (sexually produced) founding polyp, coral colonies grow by asexual reproduction (**Figure 7.7**). Each individual polyp in a colony is produced when a multicellular bud splits off from a parent polyp to form a new polyp; as a result, each polyp is a genetically identical copy, or *clone*, of the founding polyp. Once the colony has grown to a certain size and conditions are right, the polyps reproduce sexually, producing offspring that develop into polyps that start their own new colonies of clones.

SEXUAL REPRODUCITON AND ANISOGAMY Most plants and animals reproduce sexually, as do many fungi and protists. Some protists, such as the green alga *Chlamydomonas reinhardtii* (**Figure 7.8A**), have two different *mating types*,

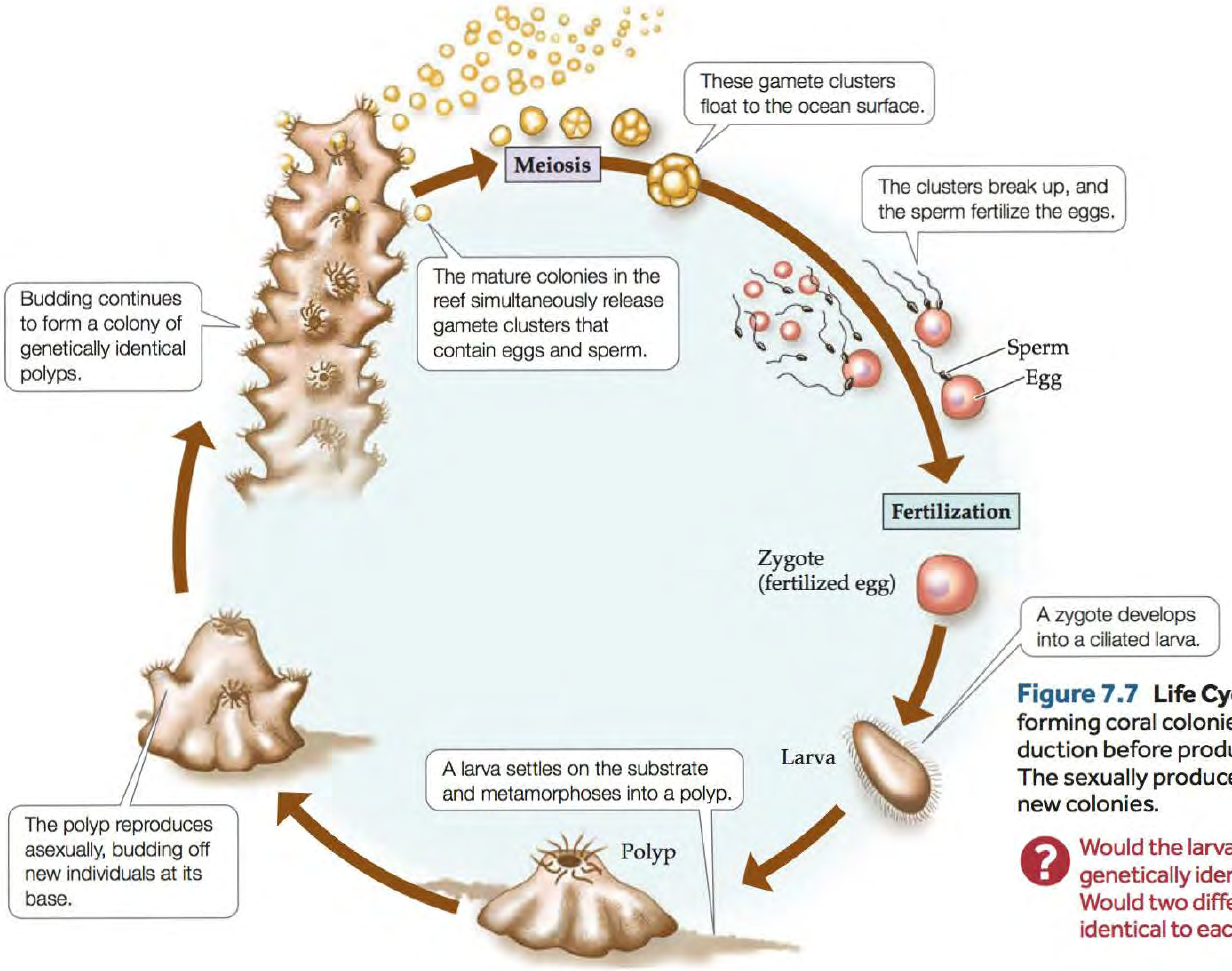


Figure 7.7 Life Cycle of a Coral Reef-forming coral colonies grow by asexual reproduction before producing eggs and sperm. The sexually produced offspring establish new colonies.

? Would the larva shown in the diagram be genetically identical to the polyp to its left? Would two different larvae be genetically identical to each other? Explain.

analogous to males and females except that their gametes are the same size. The production of equal-sized gametes is called **isogamy**. In most multicellular organisms, however, the two types of gametes are different sizes, a condition called **anisogamy**. Typically, the eggs are much larger than the sperm and contain more cellular and nutritional provisions for the developing embryo. The sperm are small and may be motile (**Figure 7.8B**). As we'll see in Concept 8.3, differences between the sexes in gamete size can influence other reproductive characteristics, such as differences between the sexes in their mating behavior.

Although sexual reproduction is widespread, it has some disadvantages. Because meiosis produces haploid gametes that contain half the genetic content of the parent, a sexually reproducing organism can transmit only half of its genetic material to each offspring, whereas asexual reproduction allows transmission of the entire genome. Another disadvantage of sex is that recombination and the independent distribution of chromosomes into gametes (during meiosis) can disrupt favorable gene combinations, potentially reducing offspring fitness. Finally,

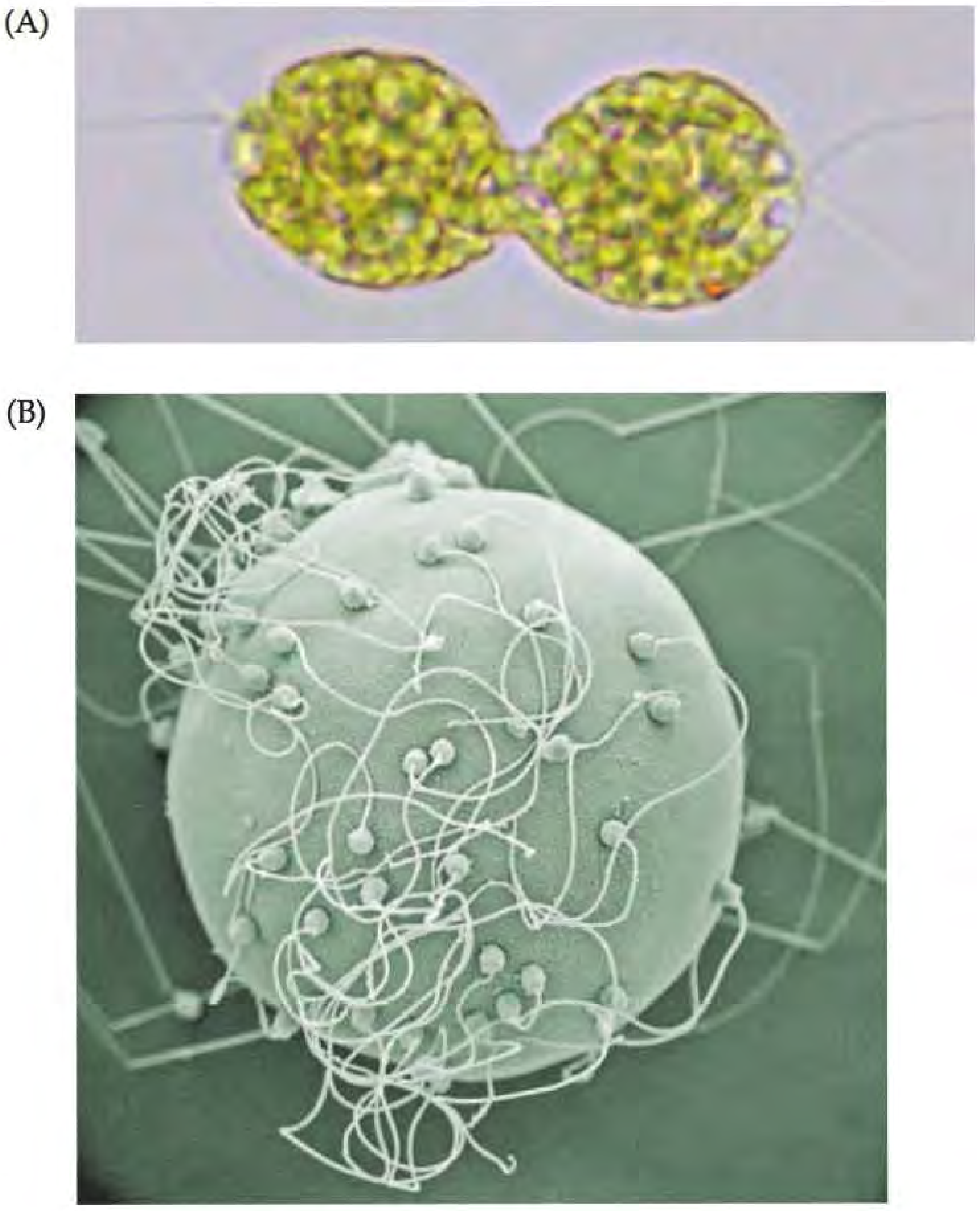


Figure 7.8 Isogamy and Anisogamy (A) An isogamous species: two gametes of the single-celled alga *Chlamydomonas* fusing. (B) An anisogamous species: fertilization of a human egg, showing the difference in size between egg and sperm.

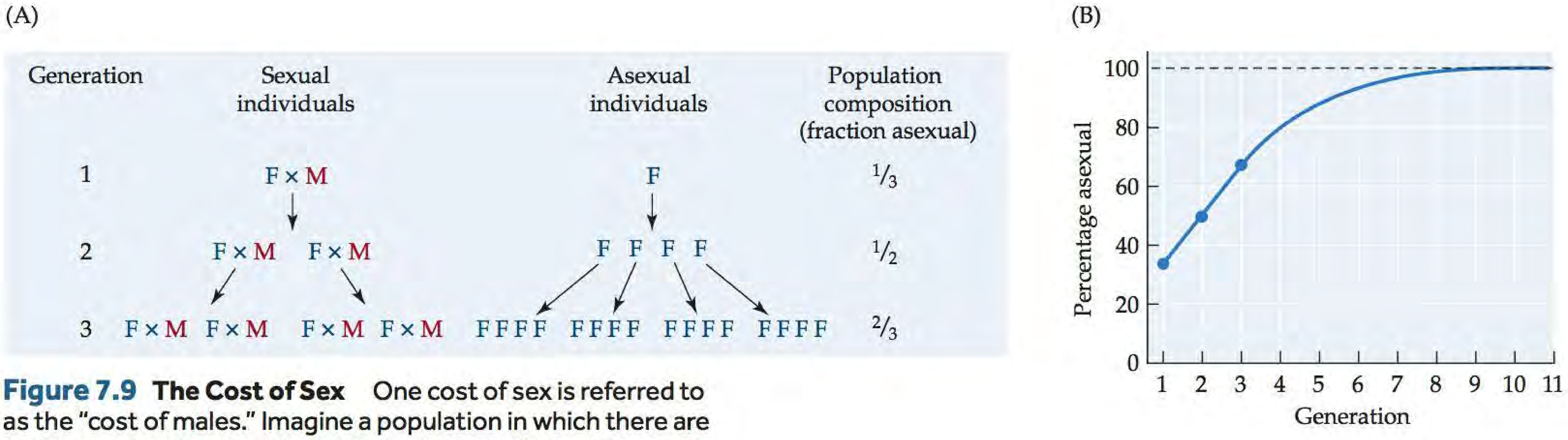


Figure 7.9 The Cost of Sex One cost of sex is referred to as the "cost of males." Imagine a population in which there are both sexual and asexual individuals. Assume that each sexual or asexual female can produce four offspring per generation, but half of the offspring produced by the sexual females are male and must pair with females to produce offspring. Under these conditions, the asexual individuals (A) will increase in number more rapidly and (B) in less than ten generations will constitute nearly 100% of the population.

? In generation 2 there are four sexual and four asexual individuals. How many sexual and asexual individuals are there in generation 3? How many of each will there be in generation 4? Explain your results in terms of the cost of males.

the growth rate of sexually reproducing populations is only half that of asexually reproducing ones, all else being equal (**Figure 7.9**).

Given such disadvantages, why is sex so common? Sex has some clear benefits, including recombination, which promotes genetic variation and hence may increase the capacity of populations to evolve in response to environmental challenges such as drought or disease. In a test of this idea, Morran et al. (2011) examined the benefits of sex in the nematode worm *Caenorhabditis elegans*. Populations of *C. elegans* consist of males and hermaphrodites. The hermaphrodites can reproduce by self-fertilization (selfing) or by mating with males (outcrossing). In wild-type populations, outcrossing rates typically range from 1% to 30%. However, *C. elegans* can be manipulated genetically to form strains that always self-fertilize ("obligate selfers") or never self-fertilize ("obligate outcrossers"). The offspring of obligate selfers are very similar genetically to their parents, whereas the offspring of obligate outcrossers are more variable genetically; thus, these strains are well suited for testing the idea that sex is beneficial because it promotes increased levels of genetic variation.

Morran et al. challenged some *C. elegans* populations by exposing them to a lethal bacterial pathogen, *Serratia marcescens*. In wild-type populations exposed to this pathogen, the rate of outcrossing increased dramatically, rising from an initial 20% to more than 80% over the course of 30 generations (**Figure 7.10A**). Moreover, *C. elegans* populations containing only obligate selfers were always driven to extinction by the pathogen, whereas wild-type and obligate-outcrossing populations always persisted (**Figure 7.10B**). Overall, these results support the hypothesis that the genetic variation generated by sex is beneficial in a challenging environment. McDonald et al. (2016) obtained similar results in yeast; moreover, they showed that sex provided benefits by increasing the fixation of advantageous mutations while decreasing the fixation of deleterious mutations.

Life cycles are often complex

The small, early stages of many animal life cycles look and behave completely differently from adult stages. They frequently eat different foods and prefer different habitats. For example, coral reef fishes such as the damselfish *Chromis atripectoralis* start life as hatchlings only a few millimeters long. The hatchlings live and grow in the open ocean, feeding on planktonic algae. When they have grown to about a centimeter in length, they return to the reef and begin to eat larger food items. This life cycle may have evolved in response to high levels of predation on young fish that stay on the reef; young fish that spend more time growing in the open ocean may have better chances of survival.

As corals (see Figure 7.7) and coral reef fishes both demonstrate, life cycles can involve stages that have different body forms or live in different habitats. A **complex life cycle** is one in which there are at least two distinct stages that differ in their habitat, physiology, or morphology. In many cases, the transitions between stages in complex life cycles are abrupt. For example, many organisms undergo **metamorphosis**, an abrupt transition in form from the larval to the juvenile stage that is sometimes accompanied by a change in habitat. As we will see in Concept 7.4, complex life cycles and metamorphosis often result when offspring and parents are subjected to very different selection pressures.

Because most vertebrates have simple life cycles that lack an abrupt transition between habitats or forms, we humans tend to think of metamorphosis as an exotic and strange process. However, complex life cycles and metamorphosis can be found even among vertebrates, including some fishes and most amphibians. Most marine

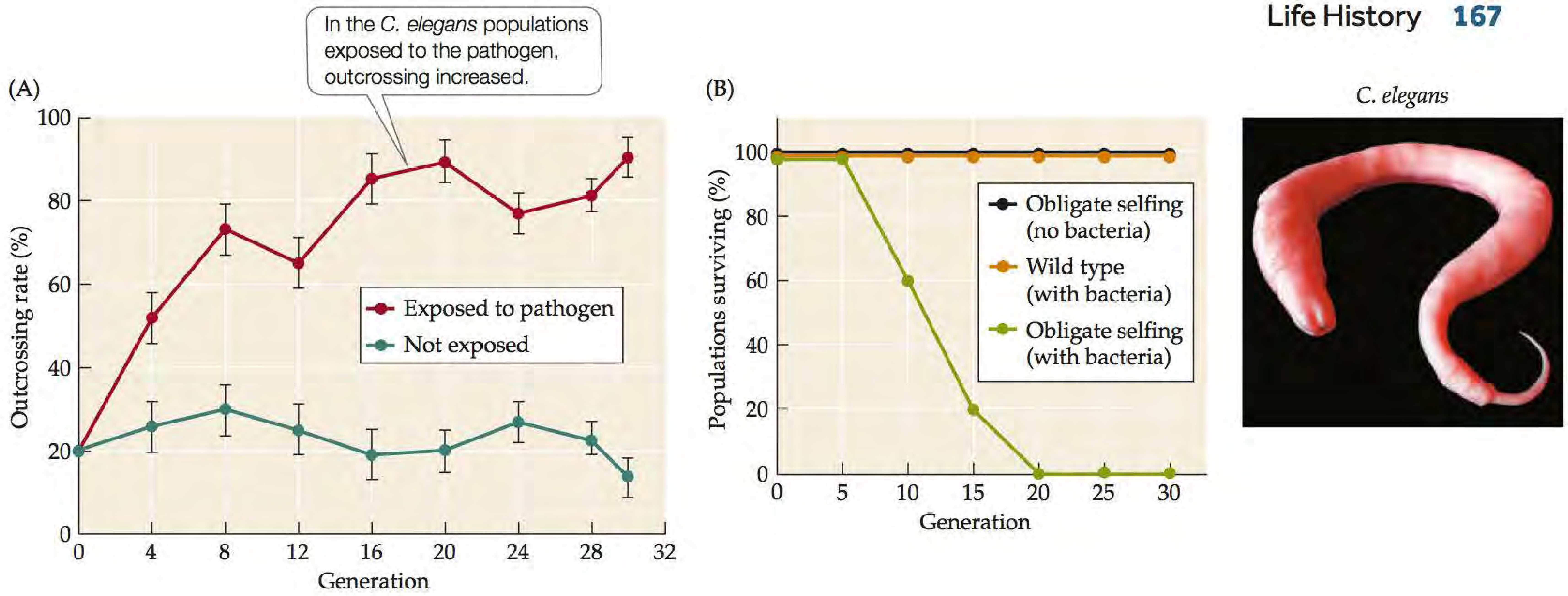

In the *C. elegans* populations exposed to the pathogen, outcrossing increased.

Figure 7.10 Benefits of Sex in a Challenging Environment (A) Outcrossing rates were measured over time in wild-type populations of the nematode worm *Caenorhabditis elegans*. Some *C. elegans* populations were exposed to the bacterial pathogen *Serratia marcescens*, while others were not. Error bars show ± one SE of the mean. (B) Percentage of replicate wild-type and obligate-selfing *C. elegans* populations surviving under different treatments. (After Morran et al. 2011.)

? In (A), which curve shows results for the control populations? Explain your choice and interpret the results shown by the two curves.

invertebrates produce microscopic larvae that swim in the open ocean before settling to the bottom at metamorphosis. Many insects also undergo metamorphosis—from caterpillars to moths, grubs to beetles, maggots to flies, and aquatic larvae to dragonflies and mayflies. In fact, Werner (1988) calculated that of the 33 phyla of animals recognized at that time, 25 contained at least some subgroups that have complex life cycles. He also noted that about 80% of all animal species undergo metamorphosis at some time in their life cycle (**Figure 7.11**).

Many parasites have evolved intricate and complex life cycles with one or more specialized stages for each host that they inhabit. For example, the parasite flatworm *Ribeiroia* has three specialized stages (see Figure 1.3). In *Ribeiroia* and other parasites, these stages are specialized to perform essential functions such as asexual reproduction, sexual reproduction, and colonization of new hosts.

Complex life cycles also occur in many types of algae and plants, reaching some of their most elaborate forms in these groups. Some algae and all plants have complex life cycles in which a multicellular diploid *sporophyte* alternates with a multicellular haploid *gametophyte*. The sporophyte produces haploid spores that disperse and grow into gametophytes, and the gametophyte produces haploid gametes that combine in fertilization to form zygotes that grow into sporophytes (**Figure 7.12**). This type of life

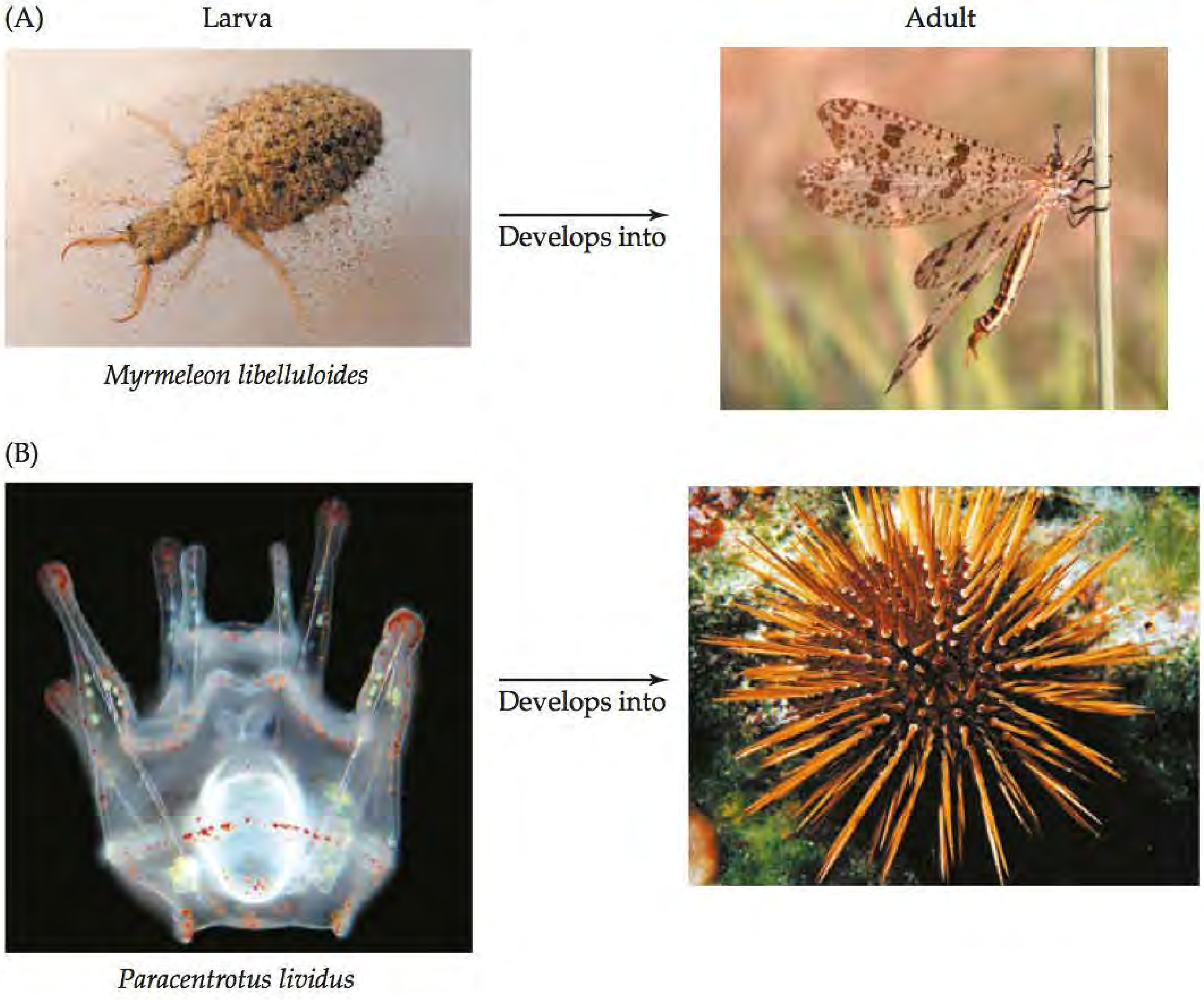
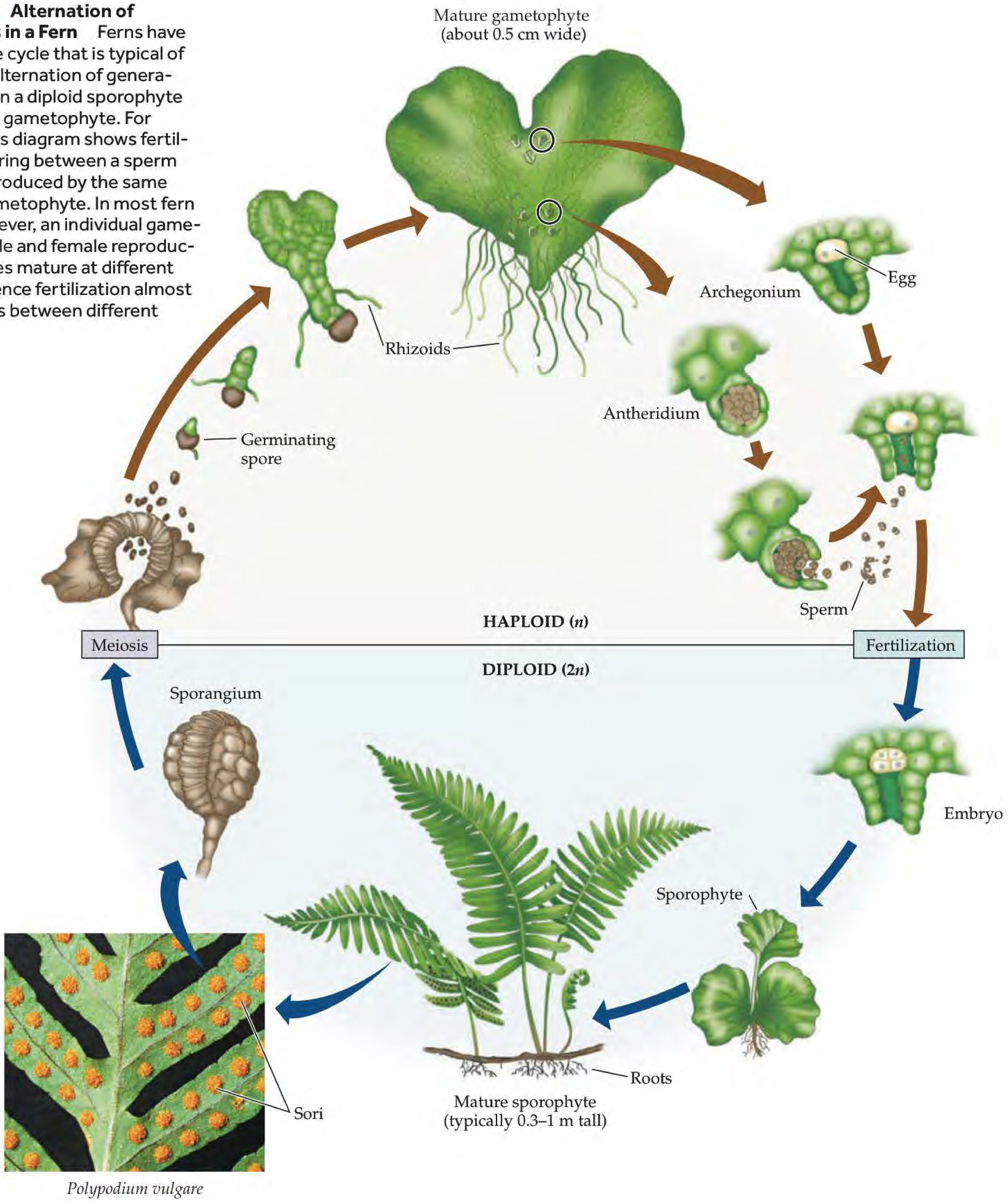


Figure 7.11 The Pervasiveness of Complex Life Cycles Most groups of animals include members that undergo metamorphosis. (A) Familiar examples are insects such as the antlion, which develops from a larva that lives in soil. (B) Most marine invertebrates have free-swimming larval stages, including echinoderms such as sea urchins.

Figure 7.12 Alternation of Generations in a Fern Ferns have a complex life cycle that is typical of plants, with alternation of generations between a diploid sporophyte and a haploid gametophyte. For simplicity, this diagram shows fertilization occurring between a sperm and an egg produced by the same individual gametophyte. In most fern species, however, an individual gametophyte's male and female reproductive structures mature at different times, and hence fertilization almost always occurs between different individuals.



cycle, called **alternation of generations**, has been elaborated on in different plant and algal groups. In mosses and a few other plant groups, the gametophyte is larger, but in most plants and some algae, the sporophyte is the dominant stage of the life cycle.

Over the course of evolution, complex life cycles have been lost in some species that are members of groups in which such cycles are considered the ancestral condition. The resulting simple life cycles are sometimes referred to as **direct development** because development from fertilized egg to juvenile occurs within the egg prior to hatching and no free-living larval stage occurs. For example, most species in one group of salamanders, the plethodontids, lack the gilled aquatic larval stage that is typical of salamanders. Instead, they lay their eggs on land, where they hatch directly into small terrestrial juveniles.

As we've seen, organisms vary greatly in key aspects of their life history strategies, such as when they reproduce, how many offspring they produce, and how much care is allotted to each offspring. How can we organize these diverse patterns into a coherent scheme?

CONCEPT 7.2

Reproductive patterns can be classified along several continua.

Life History Continua

Several classification schemes have been proposed for organizing patterns of reproduction. Most of these schemes make broad generalizations about reproductive patterns and attempt to place them along continua that are anchored by extremes at each end. Here, we examine some of the most prominent of these schemes and discuss how they relate to one another.

Some organisms reproduce only once, while others reproduce multiple times

One way of classifying the reproductive diversity of organisms is by the number of reproductive events in an individual's lifetime. **Semelparous** species reproduce only once in a lifetime, whereas **iteroparous** species have the capacity for multiple bouts of reproduction.

Many plant species typically complete their life cycle in a single year or less. Known as *annual plants*, such species are semelparous: after one season of growth, they reproduce once and die. A more complex example of a semelparous plant is the century plant (a common name applied to several species in the genus *Agave*) of North American deserts. These plants have a prolonged stage of vegetative growth that lasts up to 30 years before undergoing a single intensive bout of sexual reproduction. When it is ready to reproduce, a century plant produces a single stalk of flowers that is up to 6 m (20 feet) tall and towers over the rest of the plant. After pollination, the flowers produce clumps of seeds that drop off and take root around the parent plant. The portion of the plant that produced the tall stalk of flowers dies after this event; hence, it is semelparous. At the genetic level, however, a century plant individual does not die when it flowers, because the plant also reproduces asexually, producing genetically identical clones that surround the original plant (**Figure 7.13**). In this sense, century plants are not semelparous after all—the clones survive after the flowering event and will eventually flower themselves.

A striking example of a semelparous animal is the giant Pacific octopus (*Enteroctopus dofleini*), which in its 3–5 year life span (relatively short for an octopus species) can reach about 8 m (25 feet) in length and weigh nearly 180 kg (400 pounds). The female of this marine invertebrate species lays a single clutch containing tens of thousands of fertilized eggs. She then broods the eggs for up to 6 months. During this time, the female does not feed at all; she is a constant presence over her eggs, cleaning and ventilating them. The female dies shortly after the eggs hatch, having exhausted herself in this intense period of parental investment.

Most organisms do not invest so heavily in single reproductive events. Iteroparous organisms engage in multiple bouts of reproduction over the course of a lifetime. Examples of iteroparous plants are long-lived trees such as pines and spruces. Among animals, most large mammals are iteroparous. Of course, iteroparity can take a variety of

Figure 7.13 Agave: A Semelparous Plant? The *Agave* individual that produced the tall flowering stalk will die shortly after it flowers and so can be viewed as semelparous. But the individual that flowered also produced genetically identical clonal offspring. Thus, the genetic individual will live on after flowering, and in that sense it is not semelparous after all.

forms, from plants that flower twice in a season and then die to trees that reproduce every year for centuries.

Live fast and die young, or slow and steady wins the race?

One of the best-known schemes for classifying reproductive diversity was also one of the first proposed. In 1967, Robert MacArthur and Edward O. Wilson coined the terms *r*-selection and *K*-selection to describe two ends of a continuum of reproductive patterns. The "*r*" in *r*-selection refers to the *intrinsic rate of increase* of a population, a measure of how rapidly a population can grow. The term ***r*-selection** refers to selection for high population growth rates. This type of selection can occur in environments where population density is low—for example, in recently disturbed habitats that are being recolonized. In this type of habitat, genotypes that can grow and reproduce rapidly will be favored over those that cannot. In contrast, ***K*-selection** refers to selection for slower rates of increase, which occurs in populations that are at or approaching *K*, the carrying capacity or stable population size for the environment in which they live (see Concepts 10.3 and 10.5 for in-depth discussions of *r* and *K*). *K*-selection occurs under crowded conditions, in which genotypes that can efficiently convert food into offspring are favored. By definition, *K*-selected populations do not have high population growth rates, because they are already near the carrying capacity for their environment and competition for resources can be intense.

One way to think of the *r*–*K* continuum is as a spectrum of population growth rates, from fast to slow. Organisms at the *r*-selected end of the continuum are often small and have short life spans, rapid development, early maturation, low parental investment, and high rates of reproduction. Examples of this "live fast, die young" end of the continuum include most insects, small short-lived vertebrates such as mice, and weedy plant species. In contrast, *K*-selected species tend to be long-lived, develop slowly, delay maturation, invest heavily in each offspring, and have low rates of reproduction. Examples of this "slow and steady" end of the continuum include large mammals such as elephants and whales, reptiles such as tortoises and crocodiles, and long-lived plant species such as oak and maple trees.

Like most classification schemes, the *r*–*K* continuum tends to emphasize the extremes. Most life histories are intermediate between these extremes, however, and hence the *r*–*K* approach is not informative in some situations. The distinction between *r*-selection and *K*-selection is perhaps most useful in comparing life histories in closely related species or species living in similar environments. For example, Braby (2002) compared three species of Australian butterflies in the genus *Mycalesis*. The species that occurs in the driest, least predictable habitats shows the most *r*-selected characteristics, including rapid development, early reproduction, production of many small eggs, and rapid population growth. In contrast, the two species found in more predictable, wet forest habitats have more *K*-selected characteristics.

Plant life histories can be classified based on habitat characteristics

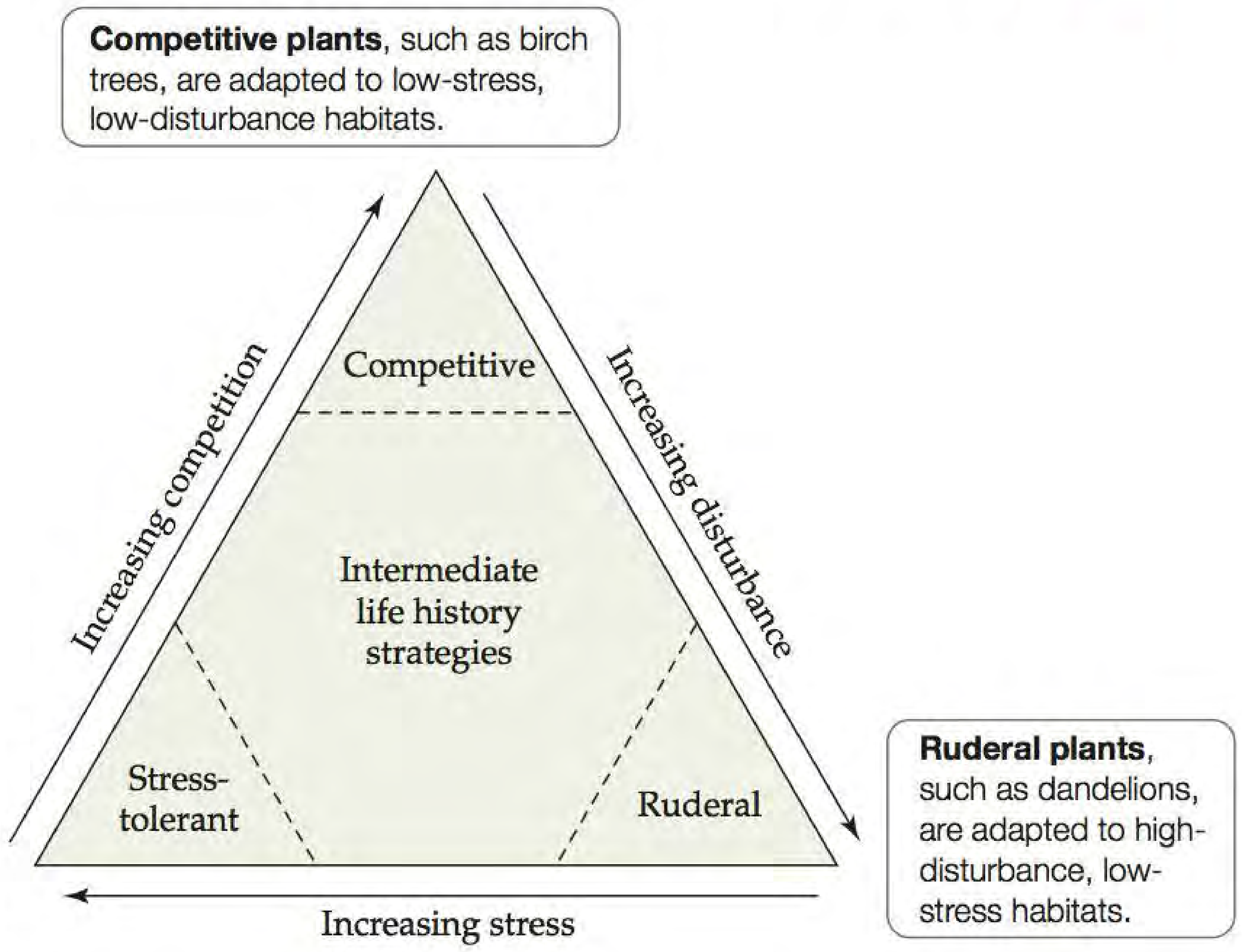
In the late 1970s, Philip Grime (1977) developed a classification system specifically for plant life histories. The success of a plant species in a given habitat, he argued, is limited by two factors: stress and disturbance. Grime defined *stress* broadly as any external abiotic factor that limits vegetative growth. Under this definition, examples of stress include extreme temperatures, shading, low nutrient levels, and water shortages. He defined *disturbance* broadly as any process that destroys plant biomass; under Grime's definition, disturbance can result from biotic sources such as outbreaks of herbivorous insects or abiotic sources such as fire.

If we consider that in a given habitat, stress and disturbance may each be either high or low, then there are four possible habitat types: high stress–high disturbance, low stress–high disturbance, low stress–low disturbance, and high stress–low disturbance. If we further consider that most habitats with high stress *and* high disturbance will not be suitable for plants, then there are three main habitat types to which plants may adapt. Grime developed a model for understanding the three plant life history patterns that correspond to these three habitat types: competitive (low stress–low disturbance), ruderal (low stress–high disturbance), and stress-tolerant (high stress–low disturbance) (**Figure 7.14**).

Grime defined competition between plants in a very specific manner as "the tendency of neighboring plants to utilize the same quantum of light, ion of a mineral nutrient, molecule of water, or volume of space." Under conditions of low stress and low disturbance, **competitive plants** that are superior in their ability to acquire light, minerals, water, and space should have a selective advantage.

Grime classified plants that are adapted to habitats with high levels of disturbance and low levels of stress as **ruderals**. The ruderal strategy generally includes short life spans, rapid growth rates, heavy investment in seed production, and seeds that can survive in the ground for long periods until conditions are right for rapid germination and growth. Ruderal species are often called "weedy" species and are adapted for brief periods of intense exploitation of favorable habitats after disturbance has removed competitors.

Finally, under conditions in which stress (in any form) is high and disturbance is low, stress-tolerant plants become ecologically dominant. Although stressful conditions may vary widely across habitats, Grime identified several features of **stress-tolerant plants**, including but not limited to slow growth rates, evergreen foliage, slow rates of water and nutrient use, low palatability to herbivores, and an ability to respond effectively to temporarily favorable



Competitive plants, such as birch trees, are adapted to low-stress, low-disturbance habitats.

Stress-tolerant plants, such as ivies, are adapted to high-stress, low-disturbance habitats.

Ruderal plants, such as dandelions, are adapted to high-disturbance, low-stress habitats.

Figure 7.14 Grime's Triangular Model Grime categorized plant life histories within a triangle whose axes indicate the degree of competition, disturbance, and stress in the habitat type to which plants are adapted. Intermediate life history strategies are shown in the center of the triangle. (After Grime 1977.)

conditions. Habitats favoring stress-tolerant plants might include places where water or nutrients are scarce or temperature conditions are extreme.

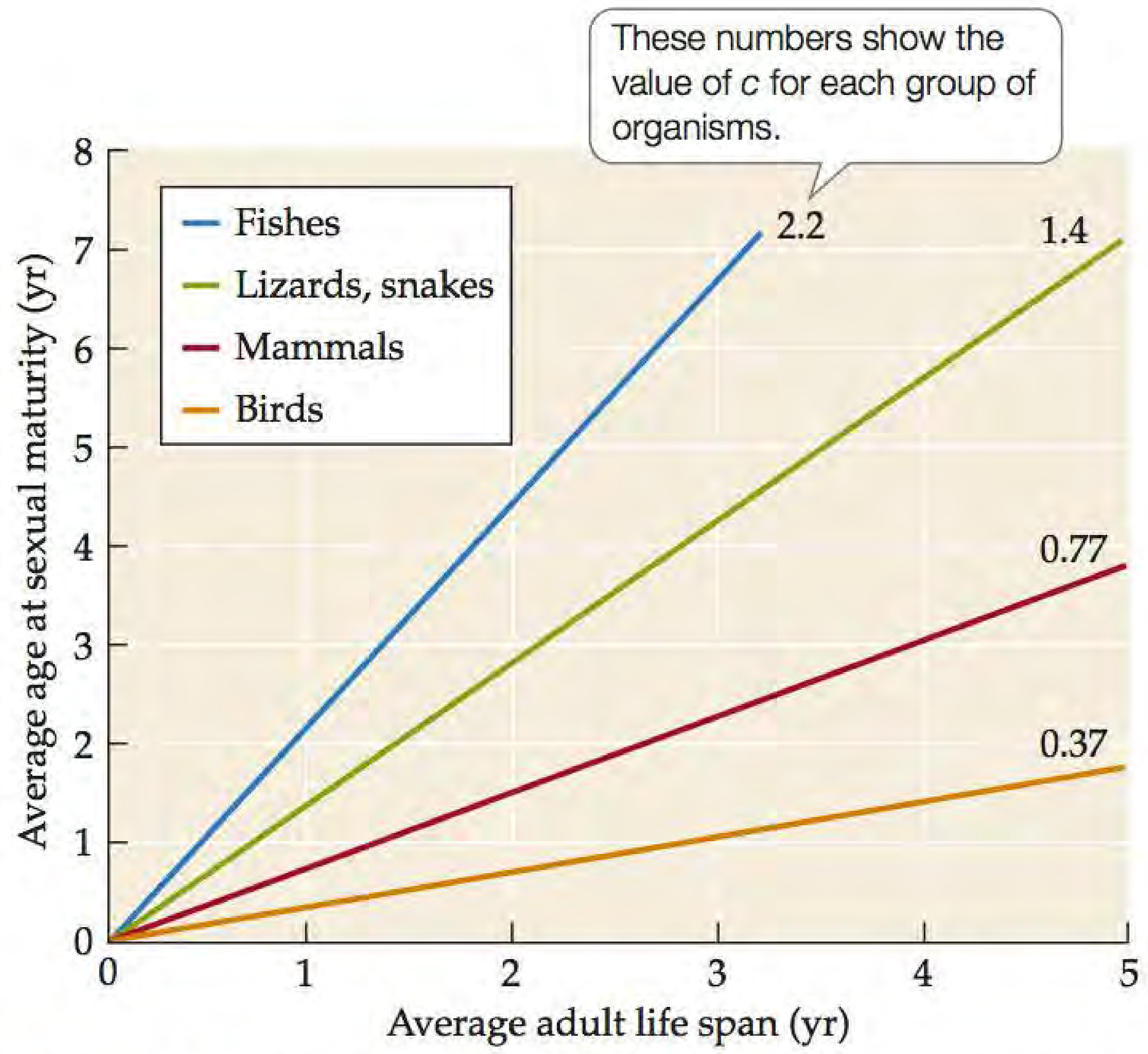
To summarize, the triangular model put forward by Grime posits that natural selection has resulted in three distinct yet very broad categories of life history strategies in plants. Although Grime focused on describing these three extreme strategies, he also recognized that intermediate strategies are commonly found. Indeed, various combinations of the three extreme strategies yield many possible intermediate strategies, such as competitive ruderals and stress-tolerant competitors, among others. Many plants fall into one of these intermediate strategies and may still be described in the context of Grime's model.

Life histories can be classified independent of size and time

Unlike the classification schemes discussed above, an approach described by Charnov (1993) organizes life histories in a manner that removes the influence of size and time. As we saw in our discussion of the *r*–*K* continuum, size and time play a critical role in traditional classifications of life histories. For example, *r*-selected species are characterized as smaller and more short-lived than *K*-selected species. But if we could control for the effects of body size and life span, then we could ask whether closely related organisms experience similar selection pressures independent of those factors.

To illustrate this approach, we'll begin with the observation that the age of sexual maturity is positively correlated with life span in many species (Charnov and Berrigan 1990). Such a correlation is not surprising: species with short life spans must mature in short periods, but the same is not true of species with long life spans; hence, a positive correlation can arise automatically. One way to remove this effect of life span is to divide the average age of maturity of a species by its average life span. This division yields a *dimensionless ratio*, that is, a ratio in which the units in the numerator (e.g., age of maturity in *years*) are identical to and hence cancel the units in the denominator (e.g., life span, also in *years*).

By removing the effects of variables such as size or (in our case) time, a dimensionless ratio allows ecologists to compare the life histories of very different organisms. Charnov and Berrigan compiled data for a wide range of bird, mammal, lizard, and fish species. To remove the effects of life span, they focused their analyses on the age of maturity:life span dimensionless ratio, which they denoted *c* (**Figure 7.15**). Their analysis revealed that *c* differed between ectothermic (fishes, lizards, and snakes) and endothermic (mammals and birds) organisms. For example, if we compare organisms with a given life span,



These numbers show the value of *c* for each group of organisms.

Figure 7.15 A Dimensionless Life History Analysis The average age at which females reach sexual maturity is plotted against the average female life span for different groups of organisms. The slope of each line yields the dimensionless ratio *c*: the average age of maturity divided by the average life span. (After Charnov and Berrigan 1990.)

? In groups of organisms for which $c > 1$, do most individuals live long enough to reproduce? Explain.

the values of *c* indicate that it takes fishes three to six times longer to mature than mammals and birds, while it takes lizards and snakes two to four times longer. Such results can highlight major differences in the life histories of different groups of organisms, thus helping to make sense of life history variation.

While this dimensionless approach has some advantages over classification schemes that incorporate time and size, it also has potential disadvantages. Indeed, an emphasis on constant or "invariant" dimensionless life history parameters has been questioned by Nee et al. (2005), who argue that life history parameters can appear to be invariant simply as an artifact of the mathematical methods used to estimate them. Overall, there are many ways to organize the vast diversity of life history strategies. The classification scheme that is most useful in any given case will depend on the organisms and questions of interest. For example, the *r–K* continuum has a long history of use in relating life history characteristics to population growth characteristics, whereas Grime's scheme may be most appropriate for life history comparisons between groups of plants. Alternatively, dimensionless analyses may be most helpful when comparing life histories across broad ranges of taxonomy or size.

CONCEPT 7.3
There are trade-offs between life history traits.

Trade-Offs

As suggested by the maxim "There is no free lunch" (see Table 1.1), no organism can invest unlimited amounts of energy in growth and reproduction. As discussed in Concept 6.3, *trade-offs* occur when organisms allocate their limited energy or other resources to one structure or function at the expense of another. As we'll see, trade-offs among life history traits are common.

There is a trade-off between number and size of offspring

Many organisms show a trade-off between their investment in each individual offspring and the number of offspring they produce. Investment in offspring includes energy, resources, time, and the loss of chances to engage in alternative activities such as foraging. In many cases, organisms that make a large investment in each offspring produce small numbers of large offspring, while organisms that make a small investment in each offspring produce large numbers of small offspring. As we'll see, parental investment can also affect offspring "quality," as when reduced investment per offspring increases the risk of offspring mortality.

LACK CLUTCH SIZE A classic example of the trade-off between investment per offspring and number of offspring was first described by David Lack in 1947. Lack asserted that clutch size in birds (the number of eggs per reproductive bout) is limited by the maximum number of young that the parents can raise at one time. If the parents rear fewer than this maximum number, they will reduce their genetic representation in future generations. If they attempt to rear more than this maximum number, their offspring may be more likely to starve or die from other causes, again reducing the parents' fitness.

Lack made careful observations of the breeding biology of bird species, from the poles to the tropics. What struck him was that clutch size varied with latitude: at higher latitudes, birds could rear greater numbers of offspring. He hypothesized that the reason for larger clutches at higher latitudes was that such latitudes had longer periods of daylight during the breeding season. These longer days allowed parents more time for foraging, and they could therefore feed greater numbers of offspring.

The term "Lack clutch size" refers to the maximum number of offspring that a parent can successfully raise to maturity. Lack hypothesized that this most productive clutch size should be the clutch size that is most commonly observed in nature. Clutch size in birds can be manipulated by the addition and removal of eggs in order to examine whether there are costs to unusually large clutch sizes. For example, Nager and colleagues (2000)

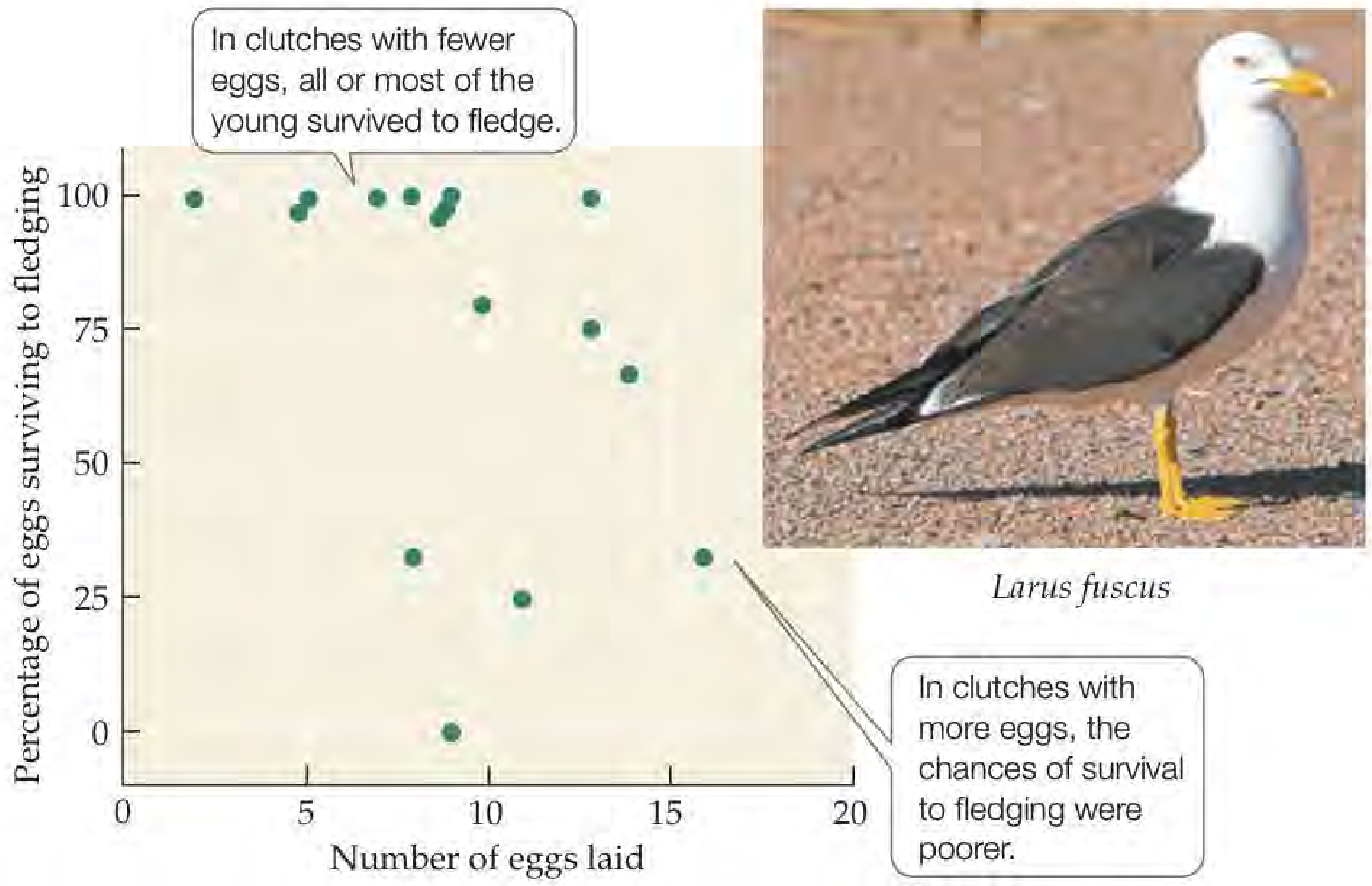
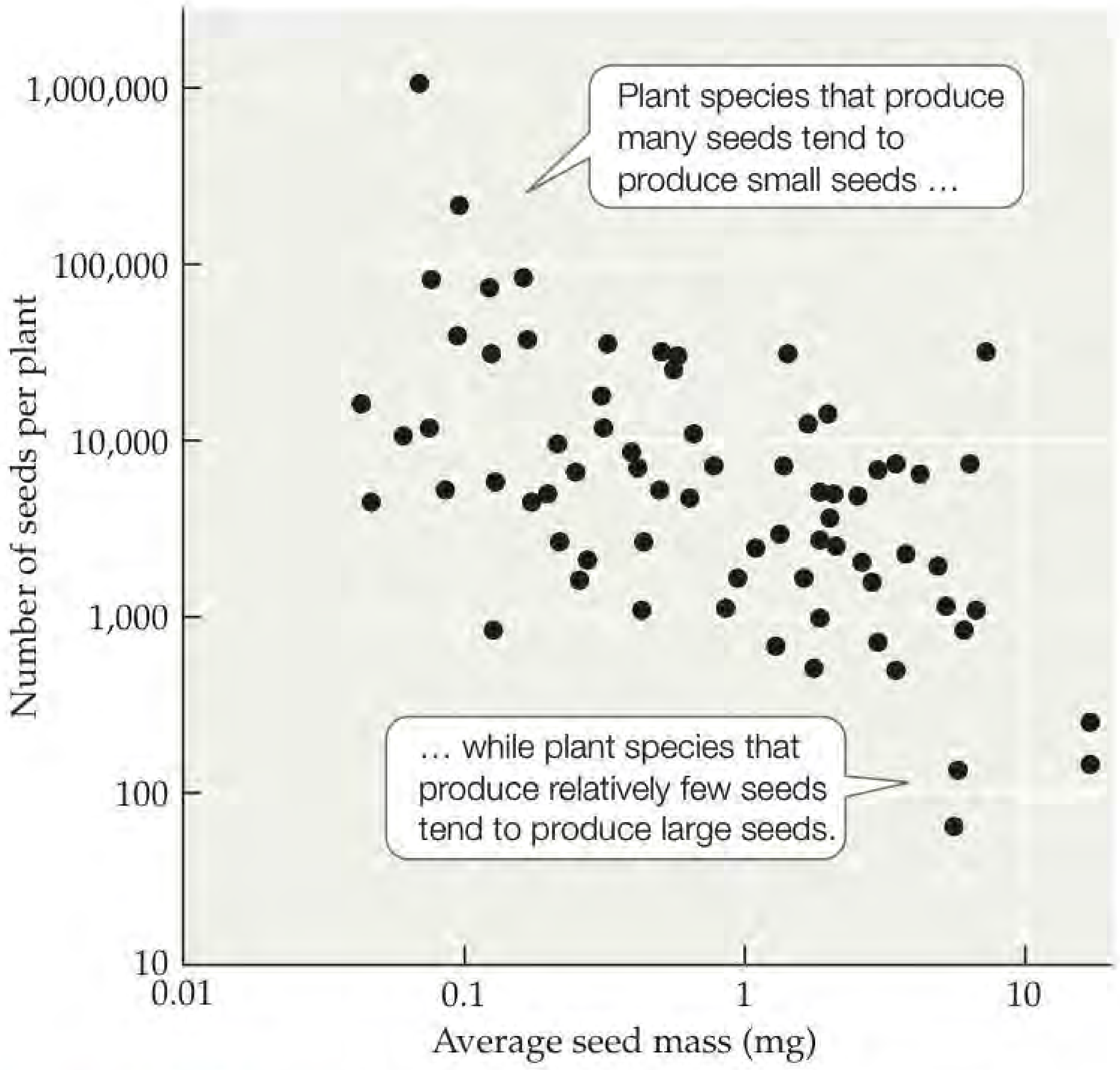


Figure 7.16 Clutch Size and Survival Lesser black-backed gulls typically lay three eggs in a clutch. However, when they are manipulated experimentally to produce larger clutches of eggs, their offspring have reduced chances of survival to fledging. (After Nager et al. 2000.)

artificially increased the number of eggs in clutches laid by the lesser black-backed gull (*Larus fuscus*). They did this by removing eggs from nests, which stimulated the females to lay more eggs. Nager et al. found that the increased clutch size resulted in a drop in the nutritional quality of later-produced eggs (specifically, these eggs had a lower lipid content). To examine the consequences of this change, they performed an experiment in which eggs from clutches of different sizes were reared singly by foster parents. Eggs from larger clutches had reduced survivorship to fledging (the point at which wing feathers are developed enough for flight) (**Figure 7.16**). Thus, in lesser black-backed gulls, production of larger clutches reduced both egg quality and survivorship to fledging.

TRADE-OFFS IN ORGANISMS WITHOUT PARENTAL CARE Parental care like that provided by birds and some other vertebrates is relatively rare. In organisms that do not provide parental care, resources invested in *propagules* (such as eggs, spores, or seeds) are the main measure of reproductive investment. In this case, the size of the propagule is the primary measure of parental investment, and propagule size is traded off against the number of propagules produced in a reproductive bout. In plants, for example, the size of the seeds that a species produces is negatively correlated with the number of seeds it produces (**Figure 7.17**).

In some cases, the size–number trade-off also applies to variation within species. The western fence lizard (*Sceloporus occidentalis*), which is common throughout the coastal mountains of the western United States, does not provide parental care. Barry Sinervo (1990) found that lizard populations farther to the north laid more eggs per clutch (Washington: 12 eggs/clutch vs. California: 7 eggs/clutch) but laid smaller eggs (Washington: 0.40 g vs. California: 0.65 g) (**Figure 7.18**).

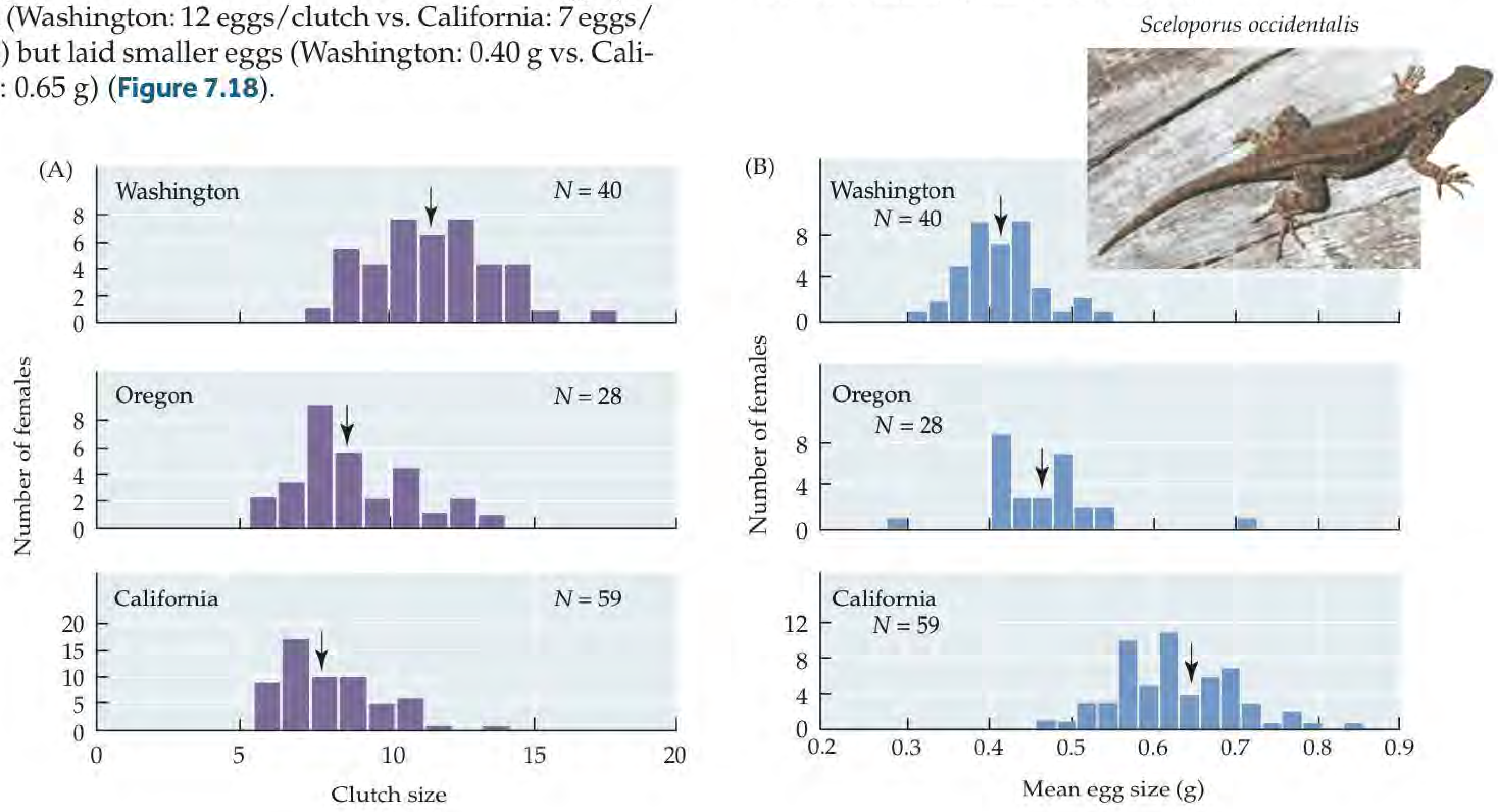


Plant species that produce many seeds tend to produce small seeds ...

... while plant species that produce relatively few seeds tend to produce large seeds.

Figure 7.17 Seed Size–Seed Number Trade-Offs in Plants (After Stevens 1932.)

Figure 7.18 Egg Size–Egg Number Trade-Off in Fence Lizards Western fence lizards in northern populations produced (A) larger clutches and (B) smaller eggs than those in southern populations. The arrow points to the average for each population. (After Sinervo 1990.)



In order to determine the consequences of egg size for offspring performance, Sinervo raised fence lizard eggs in the laboratory. He artificially reduced the size of some of the eggs by using a syringe to remove some yolk from them. To control for any possible effects of this method on egg development, he inserted a syringe into some other eggs but did not remove any yolk. These eggs that had been poked, but not reduced, developed at the same rate as unmanipulated eggs, indicating that insertion of the syringe was not the cause of differences between unmanipulated and reduced eggs.

Sinervo found that the reduced eggs developed faster than the unmanipulated eggs but produced smaller hatchlings. These small hatchlings grew faster than their larger siblings, but they were not able to sprint as fast to escape from predators. Many of the differences between the lizards hatched from the reduced eggs and from the unmanipulated eggs echoed observed differences between populations with naturally differing egg sizes. Sinervo speculated that the differences between populations in egg and hatchling size may be the result of selection favoring faster sprint speeds in the south, where there may be more predators, or of selection favoring earlier hatching and faster growth in the north, where the growing season is shorter.

There are trade-offs between current reproduction and other life history traits

As we've seen, when parents produce more offspring, their investment per offspring may decline. Such a decline can have various effects on the offspring, including reduced survival (as in lesser black-backed gulls) and reduced size (as in western fence lizards). The allocation of resources to reproduction can also affect the parent. Indeed, allocating resources to reproduction can decrease an individual's growth rate, its survival rate, or its potential for future reproduction.

For example, a trade-off between current reproduction and survival has been documented in studies that examine how life history traits differ among species. In one such study, Ricklefs (1977) observed a trade-off between annual fecundity (as measured by the number of offspring raised to maturity) and annual survivorship in birds (**Figure 7.19A**). Trade-offs between reproduction and survival have also been observed within a species. For example, in the fruit fly *Drosophila melanogaster*, males spend more time and energy courting unmated females than they spend courting recently mated females. Partridge and Farquhar (1981) tested whether such differences in courtship activity affected the longevity of male fruit flies. Males were kept with eight virgin females per day or with eight previously inseminated females per day. In the absence of sexual activity, a male's life span is correlated positively with his size, so Partridge and Farquhar also recorded the size of each male. Among males of any particular size, males kept with virgin females had a shorter life span than did males kept with inseminated females (**Figure 7.19B**), showing a cost (reduced life span) of sexual activity among males of this species.

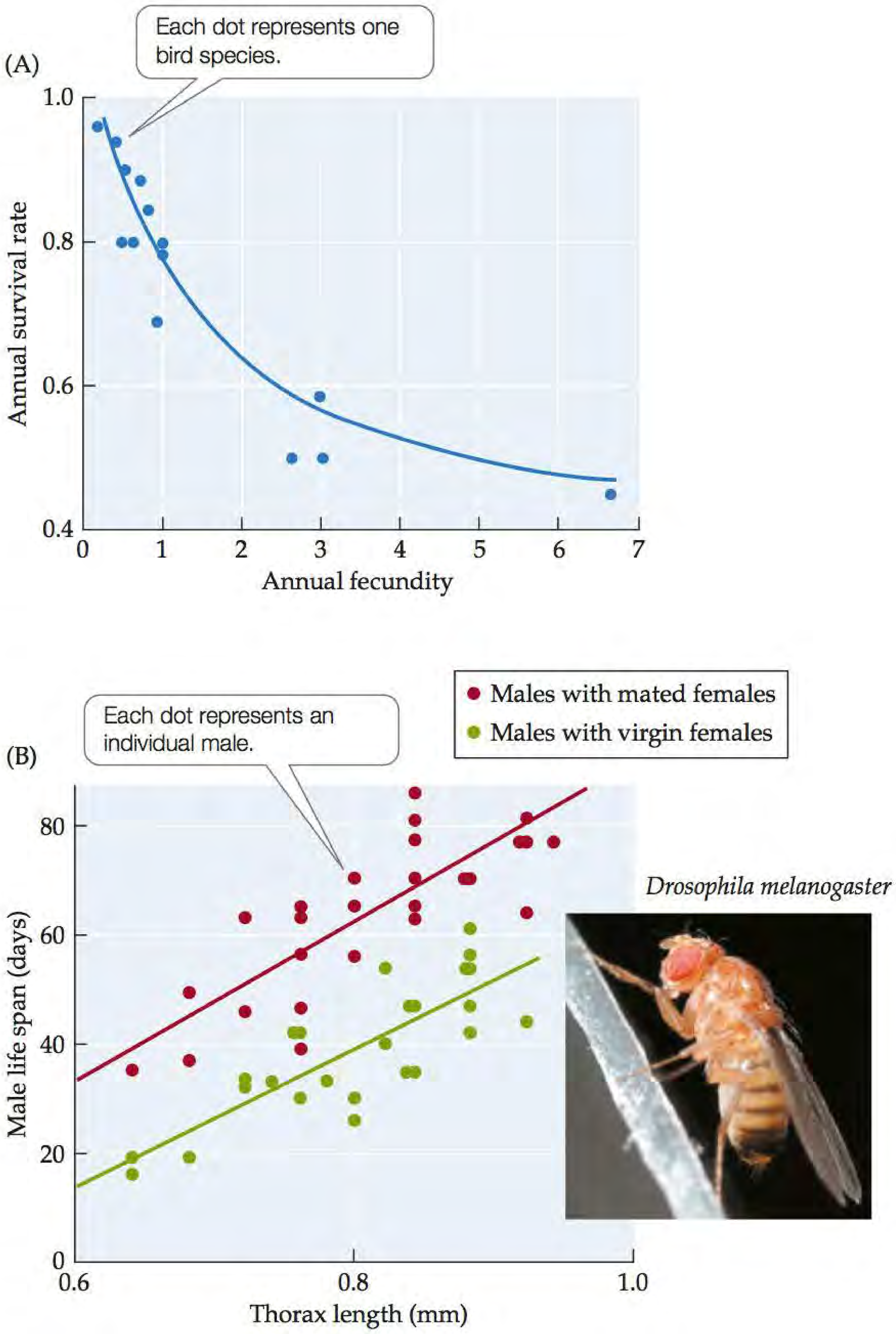


Figure 7.19 Trade-Offs between Reproduction and Survival (A) In a comparison of 14 different bird species, the annual survival rate declines as annual fecundity increases. (B) Life span versus size (thorax length in millimeters) for male *Drosophila* kept with eight virgin females or eight previously mated females. Regression lines represent average male life spans. (A after Ricklefs 1977; B after Partridge and Farquhar 1981.)

? In (B), what is the average life span of male flies with a 0.8 mm thorax kept with virgin females? How does this compare with that of males of the same size kept with previously mated females?

Similarly, evidence for a trade-off between current reproduction and growth has been found in mollusks, insects, mammals (including humans), fishes, amphibians, and reptiles (see citations in Barringer et al. 2013). A trade-off between reproduction and growth has also been observed in many plants, including Douglas fir trees (*Pseudotsuga menziesii*) (**Figure 7.20**). Note that by allocating resources to reproduction instead of growth, an individual will reproduce at a smaller size than it would if it had continued to grow and reproduced at a later time (when it was larger). Small individuals often produce fewer offspring than do large individuals, so this observation suggests that allocating resources to current reproduction might decrease an individual's potential for future reproduction. This trade-off has also received empirical support, as you can explore in **Analyzing Data 7.1**.

CONCEPT 7.4

Organisms face different selection pressures at different life cycle stages.

Life Cycle Evolution

In Concept 7.1, we saw that an organism's size may vary greatly over the course of its life cycle. This variation leads to differences among life cycle stages in habitat, food preferences, and vulnerability to predation. These differences suggest that different morphologies and behaviors are adaptive at different life cycle stages. Differences in selection pressures over the course of the life cycle are responsible for some of the most distinctive patterns in the life histories of organisms.

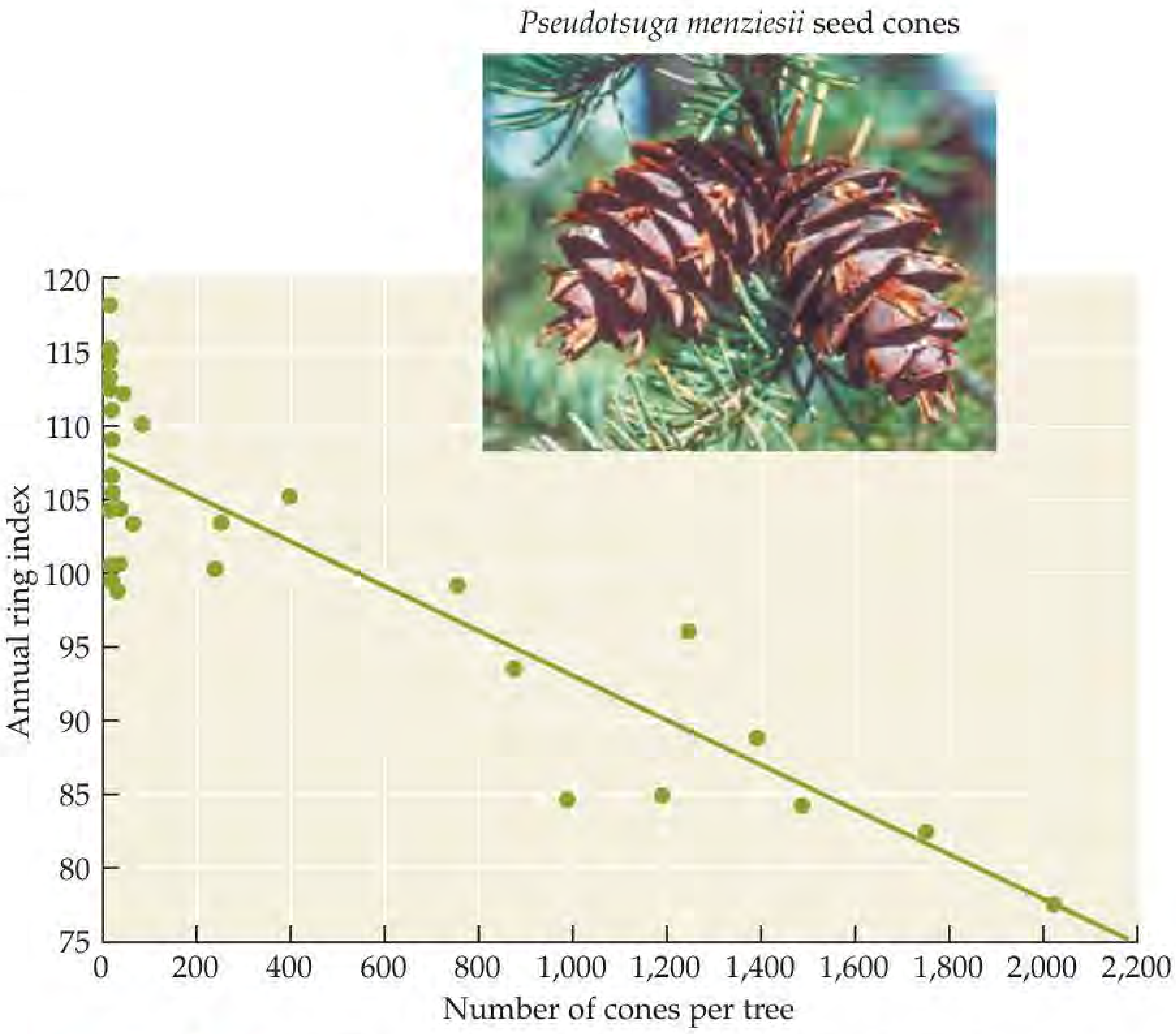

Pseudotsuga menziesii seed cones

Figure 7.20 A Reproduction versus Growth Trade-Off The thickness of annual growth rings (a measure of trunk diameter) declines in Douglas fir trees that produce many cones. (After Eis et al. 1965.)

Small size has benefits and drawbacks

Small, early life cycle stages are particularly vulnerable to predation because there are many predators that are

ANALYZING DATA 7.1 Is There a Trade-Off between Current and Delayed Reproduction in the Collared Flycatcher?

Lars Gustafsson and Tomas Pärt (1990)* studied a population of collared flycatchers (*Ficedula albicollis*) on the Swedish island of Gotland. Gustafsson and Pärt monitored the survival and reproduction of each bird throughout its entire life. They noted that some females reproduced for the first time when they were 1 year old ("early breeders"), while others reproduced for the first time when they were 2 years old ("late breeders"). The average number of eggs laid by early breeders and late breeders are reported in the table.

	AVERAGE NUMBER OF EGGS	
AGE (YEARS)	EARLY BREEDERS	LATE BREEDERS
1	5.8	—
2	6.0	6.3
3	6.1	7.0
4	5.7	6.6

1. Graph the average number of eggs (on the *y* axis) versus age (on the *x* axis) for both early breeders and late breeders.
2. Do the results suggest that it would be advantageous for birds to delay reproduction until they were 2 years old? Explain.
3. Do the results indicate that allocating resources to current reproduction can reduce an individual's potential for future reproduction? Explain.
4. These results were based on field observations. What are the limitations of such data? Propose an experiment to test whether there is a cost of reproduction in females that reduces their potential for future reproduction.

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*Gustafsson, L. and T. Pärt. 1990. Acceleration of senescence in the collared flycatcher *Ficedula albicollis* by reproductive costs. *Nature* 347: 279–281.

See the companion website for a similar ANALYZING DATA exercise.

big enough to consume them (although for some predators, small prey may be more difficult to detect). These small stages may also be poor competitors for food and thus more susceptible to environmental perturbations that diminish food supply, because they have little storage capacity for nutrients to help them withstand starvation. These vulnerabilities are typically counterbalanced by behavioral, morphological, and physiological adaptations. Furthermore, in some organisms, small, mobile early stages can perform essential functions that are not possible for large adult stages. Here, we examine how organisms protect small life history stages and the important functions those stages can provide.

PARENTAL INVESTMENT In many organisms, the parents' main investment in their offspring is the provisioning of the eggs or embryos. Animals add yolk to their eggs, which helps their offspring survive and grow through the small, vulnerable stages of life. Female kiwis, for example, produce one very yolky egg at a time; the egg is so large that it makes up 15%–20% of the bird's body size (**Figure 7.21**). During the month that it takes her to make the egg, the female kiwi eats about three times as much as when she is not producing an egg. In many invertebrate groups, species with yolkier eggs develop more rapidly, and require less food during development, than those with less yolky eggs. Another pattern common among invertebrates is investment in energetically expensive egg capsules that protect the offspring during development. Plants provision the fertilized embryos in their seeds with *endosperm*, nutrient-rich material that sustains the developing embryo and often the young seedling. The starchy white part of corn kernels and the milk and meat of coconuts are examples of endosperm.

Another mechanism for protecting small, vulnerable offspring is parental care. Birds and mammals are the most familiar examples of parental care because they invest large amounts of time and energy in protecting and feeding their relatively helpless offspring. Some fishes, reptiles, amphibians, and invertebrates also guard or brood their embryos and hatchlings, protecting them until they are big enough to be less vulnerable.

DISPERSAL AND DORMANCY Although small offspring are vulnerable to many hazards, they are also well suited for several important functions, including dispersal and dormancy. **Dispersal**—the movement of organisms or propagules from their birthplace—is a key feature in the life history of all organisms. Even in organisms such as plants, fungi, and many marine invertebrates that are sessile or move very little as adults, the life cycle typically includes a stage in which dispersal occurs. The small pollen, seeds, spores, or larvae of these organisms can be carried long distances by water or wind or, in the case of pollen and seeds, by animals. In general, smaller propagules disperse more readily and can travel farther in a given amount of time.

Figure 7.21 Kiwi Parental Investment This X-ray photograph shows the size of a kiwi egg in proportion to the female's body size. (Courtesy of the Otorohanga Zoological Society.)

Dispersal provides a number of potential advantages: for example, it can reduce competition among close relatives, and it can allow organisms to reach new areas where they can grow and reproduce. In some circumstances, dispersal can increase the chance of escaping regions of high mortality, as when pathogens and other natural enemies are abundant at the location from which organisms disperse.

The ability of an organism to disperse can also have important evolutionary consequences. For example, Hansen (1978) compared the fossil records of extinct marine snails with typical swimming larvae with those of species that had lost their swimming larval stages and developed directly into crawling juveniles. He found that the species without swimming larvae tended to have smaller geographic distributions and were more prone to extinction (**Figure 7.22**). Hansen attributed these differences to differences in dispersal ability. Species with swimming larvae would have been able to move greater distances and hence would have had more broadly distributed populations that were less vulnerable to random events that could lead to extinction.

Small size also makes eggs and embryos well suited to *dormancy*: a state of suspended growth and development in which an organism can survive unfavorable conditions. Many seeds are capable of long periods of dormancy before germination. Many bacteria, protists, and animals can also undergo various forms of dormancy. The brine shrimp eggs that children purchase as "sea monkeys," for example, are in a dormant state that allows them to survive out of water, often for years. In general, small seeds, eggs, and embryos are better suited to dormancy than large multicellular organisms because they

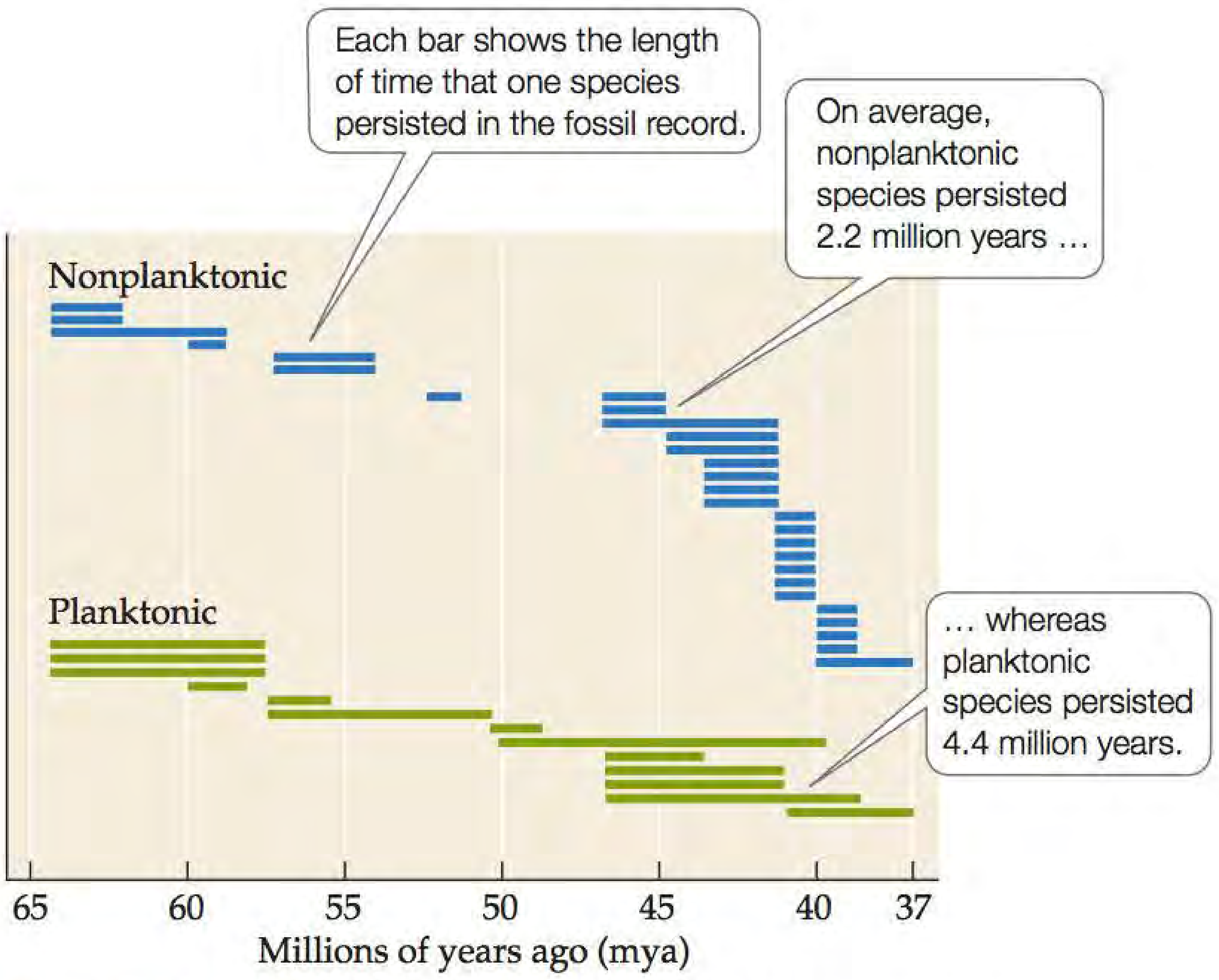


Figure 7.22 **Developmental Mode and Species Longevity** Species of marine snails that undergo direct development without a swimming larval stage (nonplanktonic) have become extinct more rapidly than those with swimming larvae (planktonic). (After Hansen 1978.)

do not have to expend as much metabolic energy to stay alive. However, some animals do enter dormancy in mature stages in response to stressful environmental conditions (as described in Concept 4.2).

Complex cycles may result from stage-specific selection pressures

Organisms with complex life cycles have multiple life stages, each adapted to its habitat and habits. This flexibility may be one of the reasons that complex life cycles are so common in so many groups of organisms. Because separate life history stages can evolve independently in response to size- and habitat-specific selection pressures, complex life cycles can minimize the drawbacks of small, vulnerable early stages.

LARVAL FUNCTION AND ADAPTATION Functional specialization of particular life stages is a common feature of complex life cycles. Having multiple stages with largely independent morphological features can result in a pairing of particular functions with particular stages. Such a pairing can reduce some of the trade-offs that result from simultaneously optimizing multiple functions.

An example of this type of specialization occurs in many insects with complex life cycles. Such insects spend their entire larval stage in a very small area—sometimes on a single plant. Insect larvae such as caterpillars and grubs are specialized eating and growing machines. They spend almost all of their time taking in food and turning it into body mass, without forming many complex morphological structures other than mandibles (chewing mouthparts or "jaws"). Once they have accumulated sufficient mass, these larvae metamorphose into adult butterflies, moths, and beetles, whose main function is often to disperse, find a mate, and reproduce. In extreme cases, such as mayflies, the adults are incapable of feeding and live only the few hours or days it takes them to reproduce.

Marine invertebrate larvae are also specialized for feeding, although they perform this function while dispersing on ocean currents. For example, the larvae of many mollusks (such as snails and clams) and echinoderms (such as sea urchins and sea stars) have intricate feeding structures that cover most of the larval body. These structures, called ciliated bands, are ridges covered in cilia that beat in coordinated patterns to catch tiny food particles and move them, like a conveyer belt, toward the mouth. The ciliated bands wind and fold their way around the larval bodies, many of which have extra lobes or arms that support and elongate the ciliated bands. In sea urchins, the longer the larval arms, and the longer the ciliated band, the more efficiently the larvae are able to feed (Hart and Strathmann 1994).

Other specialized larval structures can help to protect small life cycle stages from being eaten by other organisms. Examples include the toxin-bearing spines of some caterpillars, the head spines of crab larvae (**Figure 7.23**), and the setae or bristles of polychaete worm larvae, which deter some predators by making the larva a large and uncomfortable mouthful.

TIMING OF LIFE CYCLE SHIFTS Most organisms with complex life cycles use different habitats and food resources at different life stages. Such shifts can occur abruptly, as in organisms that undergo metamorphosis, but they can also occur more gradually. Regardless of the speed with which changes in habitat and food preferences occur, different-sized and different-aged individuals of the same

Figure 7.23 **Specialized Defensive Structures in Marine Invertebrate Larvae** The planktonic (floating) larvae of the sand crab *Corystes cassivelaunus* have defensive head spines that can make them difficult for fish to eat.

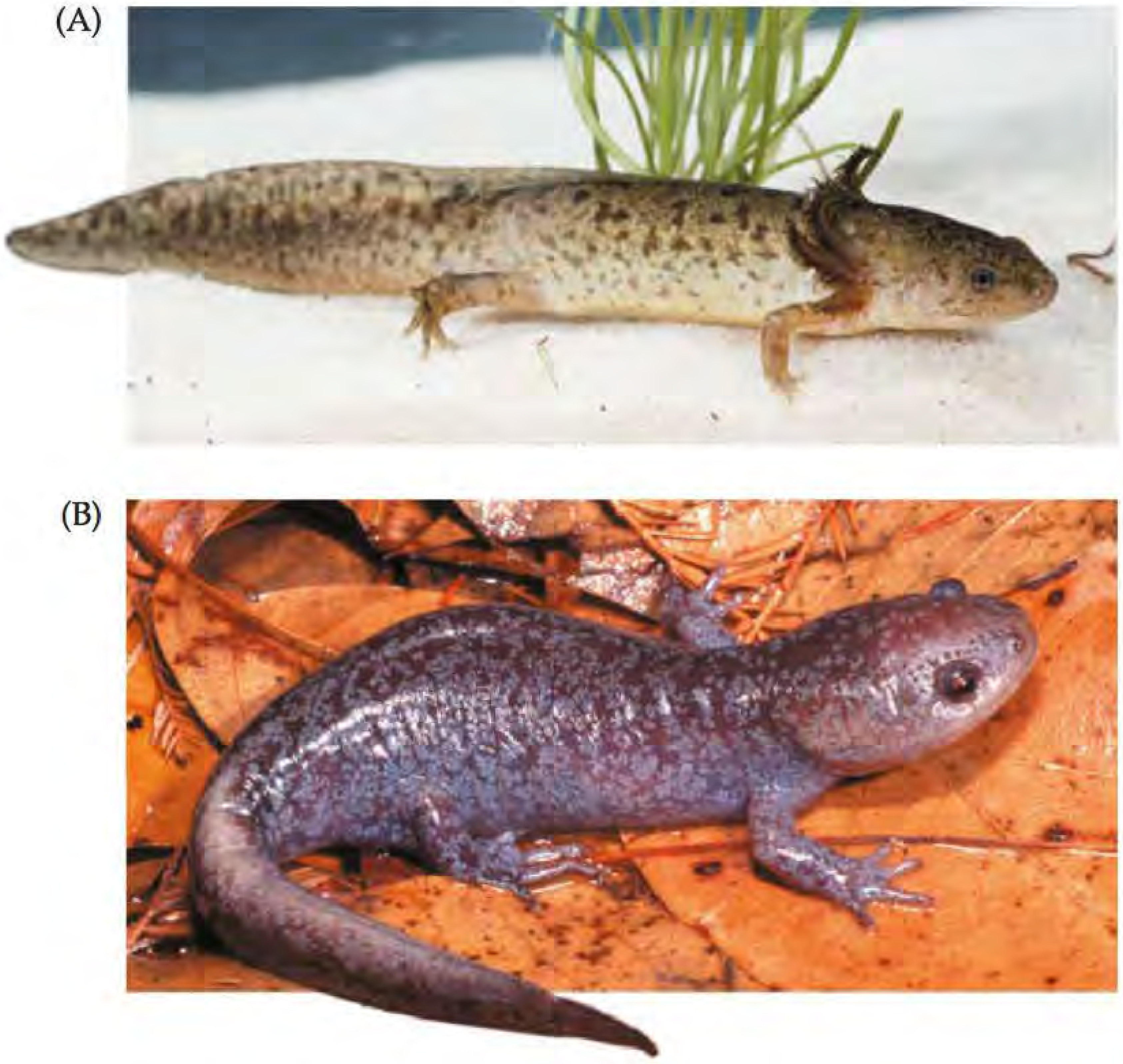


Figure 7.24 **Paedomorphosis in Salamanders** The mole salamander *Ambystoma talpoideum* can produce both (A) paedomorphic aquatic adults and (B) terrestrial metamorphic adults.

species may have very different ecological roles. We'll use the term *niche shift* to refer to such size- or age-specific changes in an organism's ecological function or habitat. (As we'll see in Concept 9.5, an organism's *ecological niche* consists of the physical and biological conditions that the organism needs to grow, survive, and reproduce.)

In species in which an abrupt metamorphosis occurs at the transition between life cycle stages, the organism spends relatively little time in vulnerable stages that are intermediate between larva and adult. In theory, there should be an optimal time to undergo metamorphosis, or any niche shift, that maximizes survival over the course of the life cycle. Thus, we might expect a niche shift to occur when the organism reaches a size at which conditions are more favorable for its survival or growth in the adult habitat than in the larval habitat.

Dahlgren and Eggleston (2000) tested this idea for the Nassau grouper (*Epinephelus striatus*), an endangered coral reef fish that spends its juvenile stages in and around large clumps of algae. Smaller juveniles spend their time hiding within the algae, whereas larger ones spend their time in rocky habitats near algal clumps. By tethering and enclosing juvenile fish of different sizes in the two habitats, Dahlgren and Eggleston were able to measure mortality and growth rates in each habitat. They found that the smaller juveniles were very vulnerable to predation in the rocky habitats, while the larger juveniles were less vulnerable and were able to grow faster in the rocky habitats. Thus, the niche shift in this species appears to be timed to maximize growth and survival, as predicted.

In some cases, the larval habitat may be so favorable for growth and survival that metamorphosis is delayed—or even eliminated altogether. For example, most salamanders have aquatic larvae that metamorphose into terrestrial adults, but some salamanders, such as the mole salamander *Ambystoma talpoideum*, can become sexually mature while retaining gills and remaining in the aquatic habitat (**Figure 7.24**). These aquatic, gilled adults are referred to as **paedomorphic**, which means that they result from a delay of some developmental events (loss of gills, development of lungs) relative to sexual maturation. In *A. talpoideum*, both aquatic paedomorphic adults and terrestrial metamorphic adults can exist in the same population. The frequency of paedomorphosis in these mixed populations seems to depend on factors such as predation, food availability, and competition—all of which influence survival and growth in the aquatic habitat.

A CASE STUDY REVISITED
Nemo Grows Up

Why does a male clownfish that has lost his mate become a female rather than simply finding a new partner? As we have seen, large individuals often produce more offspring than do smaller individuals. In clownfish, the number of eggs an individual can produce is proportional to its body

Figure 7.25 **Sequential Hermaphroditism** The slipper limpet (*Crepidula fornicata*), a marine snail, exhibits sequential hermaphroditism. Slipper limpets live in stacks attached to rocks or shells. The largest individuals, at the bottom of the stack, are females, while the smaller individuals above are males. As the males grow, they eventually reach a size (3 to 4 cm) at which they can produce more surviving offspring as females than as males; this is the size at which the sex change occurs.

size. Thus, larger individuals can produce more eggs and presumably have a better chance of having some of their offspring survive. Smaller individuals are more easily able to make sperm cells, which are smaller and take fewer resources to produce. For these reasons, in clownfish and in many other animals, females are larger than males.

Changes in sex during the course of the life cycle, called **sequential hermaphroditism**, are found in 18 fish families and in many invertebrate groups (**Figure 7.25**). Researchers have hypothesized that these sex changes should be timed to take advantage of the maximum reproductive potentials of the different sexes at different sizes, and in some cases they appear to do so. This hypothesis helps to explain sex changes in clownfish and the timing of those changes relative to size, but it leaves unanswered the question of how a hierarchy of clownfish is maintained within each anemone.

As a graduate student at Cornell University, Peter Buston set out to answer this question. He conducted experiments on a clownfish species, *Amphiprion percula*, that lives on reefs in Papua New Guinea. He found that each clownfish maintains the strict size hierarchy by remaining smaller than the fish ahead of it in line and bigger than the one behind it (**Figure 7.26**). If a fish grows to be too close in size to one of its anemone-mates, a fight results, which usually ends in the smaller fish being killed or expelled from the anemone. Buston suggested that the clownfish regulate their own growth to prevent such conflicts.

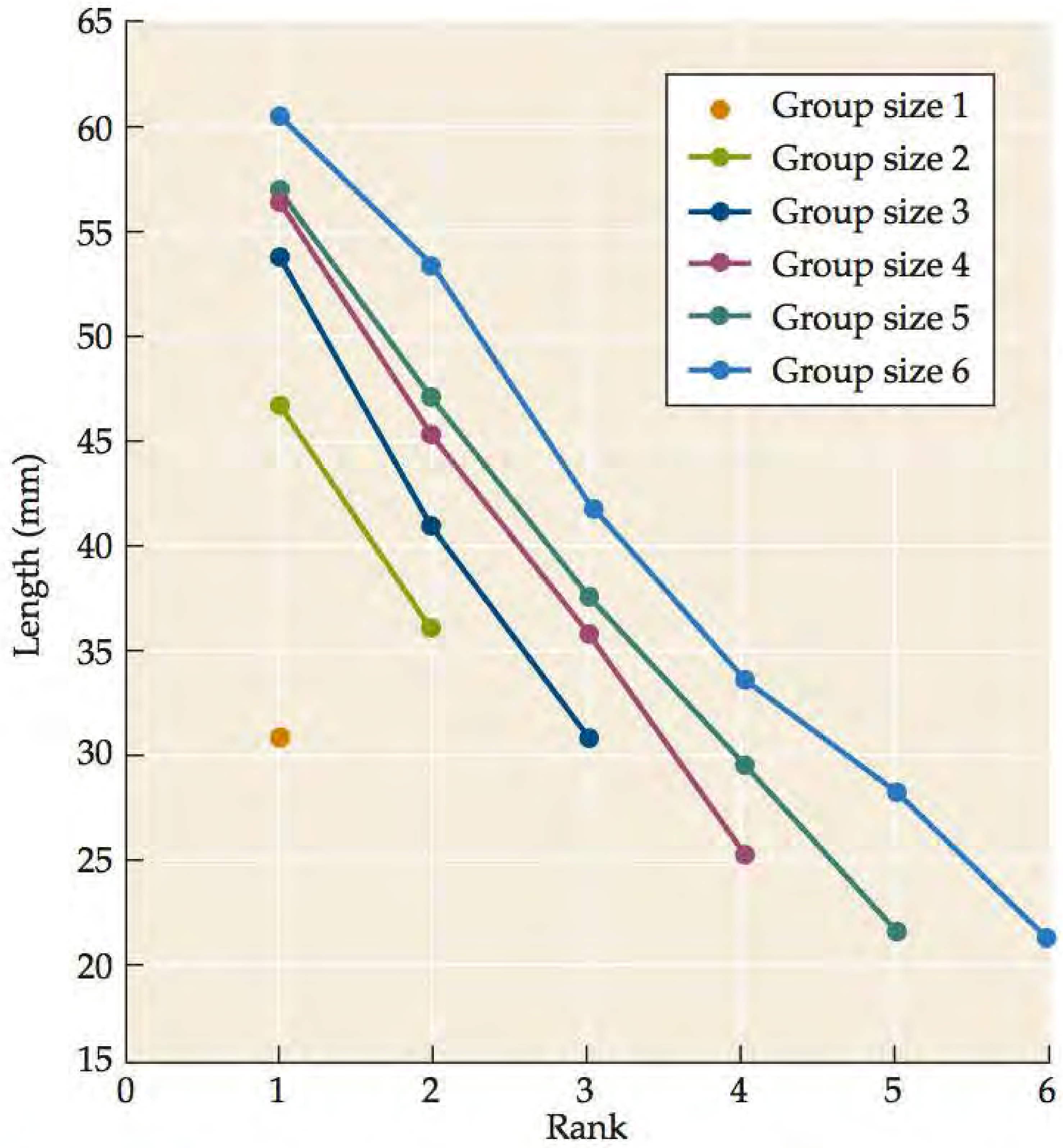


Figure 7.26 Clownfish Size Hierarchies Clownfish within an anemone regulate their growth to maintain a hierarchy in which each fish belongs to a distinct size class. Anemones may be home to between one and six fish, and the size of each fish is determined by that fish's rank and the size of the group in which it lives. (After Buston 2003a.)

Buston also manipulated clownfish groups by removing the breeding males from anemones and measuring the growth of the remaining individuals. He found that the largest nonbreeder grew only enough to take the place of the breeding male; it avoided growing too big and threatening the female's dominance. Similarly, the next largest nonbreeder grew only enough to take the place of the fish that had become the breeding male, and so on. Thus, clownfish avoid conflict within their social groups by exerting remarkable control over their growth rates and reproductive status.

CONNECTIONS IN NATURE
Territoriality, Competition, and Life History

The physiology of clownfish growth regulation is not understood, but a more pressing ecological and evolutionary question is why the size hierarchy is maintained. What makes small clownfish bide their time as nonbreeders under the dominance of a single breeding female and male? The answer may lie in the clownfish's dependence on the protection of anemones for survival.

Clownfish are brightly colored, and they are poor swimmers. Outside the anemone's stinging tentacles, they are easy prey for larger fishes on the reef. Thus, expulsion from the anemone is often a death sentence. So the stakes are very high in conflicts between fish within an anemone: the loser will probably die without reproducing. This situation exerts strong selection pressure on the fish to avoid conflicts by regulating their growth. In evolutionary terms, growth regulation mechanisms have evolved because individuals that avoid growing to a size that leads to conflict with other fish have higher survival and reproductive rates (we described this process of adaptive evolution in Concept 6.2). Buston (2003b, 2004) demonstrated that remaining in an anemone as a nonbreeder is more advantageous than trying to leave the anemone and find a new one. Anemones are a limited resource for the clownfish, and those that bide their time once they find an anemone experience the highest lifetime fitness.

The scarcity of anemones also results in competition among clownfish at a key stage in their life history. As we have seen, hatchling clownfish disperse from their anemone and spend their early life stages in the plankton. When they return to the reef, their survival depends on their choice of an anemone. The number of fish in an anemone is generally correlated with the anemone's size. However, Buston found that at any given time some anemones are undersaturated, meaning that they have room for more fish. If a juvenile fish is lucky enough to enter such an anemone, it is allowed to stay, and it enters the line of succession toward becoming a breeder. If the juvenile enters a saturated anemone, however, it is expelled, and it often dies before it can find another anemone. Similar settlement lotteries play out in many organisms that live in crowded habitats and compete for space. For example, in environments such as tropical rainforests, where many long-lived tree species compete for limited space and sunlight, the success of any one seed or seedling can depend on chance events, such as the death of a nearby large tree that creates a gap in the canopy (Denslow 1987). As we'll see in Concept 19.3, such settlement lotteries can play an important role in maintaining the diversity of species found in highly competitive environments.

Summary

CONCEPT 7.1 Life history patterns vary within and among species.

- Life histories are diverse, varying between individuals of the same species as well as between species. The source of this variation may be genetic or environmental.
- Organisms may reproduce sexually or asexually. In many cases, the same organism can do both.
- There are advantages and disadvantages to sexual reproduction. The high levels of genetic variation resulting from sexual reproduction may be beneficial in challenging environments.
- Most organisms have complex life cycles with multiple stages that differ in size, morphology, or habitat.

CONCEPT 7.2 Reproductive patterns can be classified along several continua.

- Semelparous species reproduce only once in a lifetime, while iteroparous species reproduce multiple times.
- The terms *r*-selection and *K*-selection refer to two ends of a continuum of reproductive patterns based on population growth rates.
- Grime's triangular model categorizes plant life histories by the degree of competition, stress, and disturbance in the habitat type to which they are adapted.
- Charnov's dimensionless life history analysis attempts to remove the effects of size and time in order to compare life histories across a broad taxonomic range.

CONCEPT 7.3 There are trade-offs between life history traits.

- There is a trade-off between offspring size and number, such that organisms tend to produce large numbers of relatively small offspring or small numbers of relatively large offspring.
- An individual's investment in current reproduction can result in a trade-off between reproduction and other life history traits, including survival, growth, and potential for future reproduction.

CONCEPT 7.4 Organisms face different selection pressures at different life cycle stages.

- The small sizes of early life cycle stages make them vulnerable to predation and food shortages.
- Small life cycle stages are well suited to some important functions, such as dispersal and dormancy.
- Complex life cycles allow life histories the flexibility to respond to differences in selection pressures on different life cycle stages.

Review Questions

1. Many closely related animal species produce eggs of vastly different sizes. As we saw in Concept 7.3, one trade-off of producing larger eggs is that fewer eggs can be produced. Despite the apparent simplicity of this trade-off, it is still unclear why both strategies (many small eggs and few large eggs) are maintained in groups of closely related species. What are some other life history traits besides offspring number that might be correlated with egg size, and under what environmental conditions might those traits be advantageous? Can you think of any reasons why species that live in the same habitats continue to exhibit reproductive patterns that vary so widely?
2. Some animals exhibit both sexual and asexual reproduction, depending on the environmental conditions they experience. Rotifers are a classic example of this phenomenon. Females can produce diploid eggs by mitosis that hatch soon after release. In this manner, rotifer populations can double within hours. These same females, under other conditions, can produce haploid eggs that form males if unfertilized and form females if fertilized. What might be the reason for the maintenance in rotifers of both sexual and asexual reproduction?
3. The Nassau grouper is popular in Asia where restaurant-goers can pick the grouper they want steamed for dinner from a selection of live fish swimming in tanks. Adult groupers can grow to large sizes (up to 3 feet long and 55 pounds), but those favored by restaurants are plate-sized juvenile and young adult fish. How would you expect the removal of these younger, smaller fish to affect the life history evolution of the remaining population? How might life history parameters such as age and size at reproduction and investment in growth versus reproduction evolve in response to fishing pressures?

Hone Your Problem-Solving Skills

California sheephead (*Semicossyphus pulcher*) are predatory fish that are born as females and change sex to males when they become large enough to defend territories from other males. Researchers measured the size at which sheephead became sexually mature ("size at maturation") and the size at which they changed sex from female to male ("size at sex change") for fish collected at Santa Catalina and San Nicolas Islands (Hamilton and Caselle 2015). The results are shown in the table. Little fishing occurred at these islands from 1940 to 1980. At Catalina, sheephead have been subjected to intensive fishing pressure from the early 1980s to the present. At San Nicolas, sheephead were subjected to intensive fishing from the early 1980s to 1998 but protected from fishing from 1999 on.

	CATALINA		SAN NICOLAS	
YEAR	SIZE AT MATURATION (MM)	SIZE AT SEX CHANGE (MM)	SIZE AT MATURATION (MM)	SIZE AT SEX CHANGE (MM)
1980	213	350	298	493
1998	198	256	211	294
2007	178	225	300	460

1. Do the data indicate that fishing by humans affects the sizes at which these fish reach sexual maturity and change sex? Explain.
2. Do size at maturation and size at sex change recover once fishing pressure is reduced? Explain which data you used to answer this question, and why.
3. Fishing not only reduces the abundance of the targeted species, but also tends to remove larger individuals at higher rates than smaller individuals, leading to changes such as those shown in the table. Suppose larger sheephead produce more offspring than do smaller individuals (as is true for many species). Predict how protection from fishing will affect the average number of offspring produced per female and the abundance of the population over time.

ON THE COMPANION WEBSITE

ecology4e.sinauer.com

The website includes companions to all of the Analyzing Data exercises, Online Quizzes, Flashcards, Suggested Readings, and more. In addition, the following resources are available for this chapter:

Hands-On Problem Solving

7.1 "You Can't Always Get What You Want": Life History Trade-Offs

8 Behavioral Ecology

KEY CONCEPTS

CONCEPT 8.1 An evolutionary approach to the study of behavior leads to testable predictions.

CONCEPT 8.2 Animals make behavioral choices that enhance their energy gain and reduce their risk of becoming prey.

CONCEPT 8.3 Mating behaviors reflect the costs and benefits of parental investment and mate defense.

CONCEPT 8.4 There are advantages and disadvantages to living in groups.

Baby Killers: A Case Study

Lions are unique among cats in that they live in social groups called *prides*. A typical lion pride contains anywhere from 2 to 18 adult females and their cubs, along with a few adult males. The adult females form the core of the pride, and they are closely related: they are mothers, daughters, aunts, and cousins. The adult males in a pride may be closely related as well (e.g., brothers or cousins), or they may be a coalition of unrelated individuals that help one another.

The lions in a pride hunt cooperatively, and the females often feed, care for, and protect one another's cubs. But life in a pride has a dark side as well. The male in **Figure 8.1** is killing one of the cubs in his pride, a behavior that seems both horrific and puzzling. Why do adult male lions do this? To shed light on this murderous behavior, let's consider some aspects of the life history of lions in more detail.

As young adults, male lions are driven from the pride into which they were born. A group of young males expelled from a pride may stay together to form a "bachelor pride." Bachelor prides may also consist of males from different prides that meet and begin to hunt together. By the time they are 4 or 5 years old, the young males in a bachelor pride are large and strong enough to challenge the adult males of an established pride. If their challenge is successful, the new males drive off the "dethroned" males, and they typically try to kill any young cubs that were recently fathered by those males. Although the females fight back, the new males often succeed in killing cubs.

If a female's cubs are killed, she becomes sexually receptive soon thereafter. In contrast, it can take up to 2 years for a female with cubs to resume sexual cycling. This delay in sexual receptivity can help us to understand the behavior of the incoming males. On average, incoming males remain with a pride for just 2 years before they are defeated and displaced by a new group of younger males. By killing cubs when he enters a pride, a new male increases the chance that he will reproduce before he is displaced by a younger male. As a result, incoming males that commit infanticide should leave more offspring than do males that do not commit infanticide. This logic suggests that infanticidal behavior by males is favored by natural selection, leading us to expect that it would be common in lion populations (which it is).

Figure 8.1 Killing the Cub
The male African lion shown here is attempting to kill the juvenile offspring of another male; such attempts often succeed. Why might this behavior be evolutionarily adaptive for the murdering male?

Figure 8.2 Females That Fight to Mate with Choosy Males Red phalarope (*Phalaropus fulicarius*) females (the two birds on the left) are larger and more colorful than the male of their species (on the right). In this species, the females fight over the right to mate with the males—and the males choose which females they will mate with.

Infanticide is just one of the seemingly odd behaviors we see in animals. Fruit flies, for example, sometimes lay their eggs in food sources that contain high concentrations of ethyl alcohol, a toxic substance. Why do they do this? And why is it that the females of many species are more "choosy" than the males in selecting a mate—and yet in some species, such as the birds in **Figure 8.2**, the males are choosy and the females try to mate with as many males as possible? For answers, we turn to the strange and wonderful world of animal behavior.

Introduction

In nature, many of an animal's activities are centered on obtaining food, finding mates, or avoiding predators. The behavioral decisions an animal makes often play key roles in its ability to meet these three critical needs. Consider the dilemma facing a young male lion deciding whether to challenge the adult males of a lion pride. An incorrect decision by the young male could lead to serious injury or death (if he is defeated in combat), or it could lead to a missed opportunity to join a pride and reproduce (if he delays combat unnecessarily). Likewise, a young trout that remains close to a hiding place while feeding may increase its chance of escaping predators, but in so doing, it may forgo the opportunity to forage in areas that are rich with food but lacking in protective cover.

As these examples suggest, the behavioral decisions made by individuals have very real costs and benefits that affect their ability to survive and reproduce. These examples also highlight the fact that animal behaviors take place in an ecological setting: the behavioral decisions of the lion and the trout are made in the presence of competitors and predators. As we'll see in this chapter, the facts that behaviors occur in an ecological setting and that they affect survival and reproduction are central themes in the field of **behavioral ecology**, the study of the ecological and evolutionary basis of animal behavior.

Behavioral ecology is a dynamic field, broad in scope. We cannot provide a comprehensive survey of this field in a single chapter (for that, see the textbooks on behavioral ecology listed in the Suggested Readings on the book's website). Instead, following up on the topics highlighted by life in lion prides, throughout this chapter we'll emphasize three aspects of behavior: foraging behavior, mating behavior, and living in groups. Let's begin by taking a closer look at the types of questions that behavioral ecologists address in their research.

CONCEPT 8.1

An evolutionary approach to the study of behavior leads to testable predictions.

An Evolutionary Approach to Behavior

Researchers studying animal behavior can seek to answer questions at several different levels of explanation. You might ask, for example, why a robin hopping around your yard periodically tilts its head to the side. It turns out that the bird is listening for worms moving through the soil. Robins can do this because their sensory and nervous systems can detect the faint sounds of worms moving through the soil. (You can hear those sounds in **Web Extension 8.1**.) Thus, one explanation for the robin's behavior might focus on how the required sensory equipment works. Furthermore, hunting by listening might enable a robin to detect otherwise hard-to-find prey. Hence, a second explanation of the robin's head-tilting behavior might focus on whether listening for worms increases the efficiency of foraging, thus enhancing the bird's survival and reproductive success. If so, then this behavior may have become common over time because it was favored by natural selection.

Notice that the first explanation we mentioned addresses a "how" question about behavior: it looks within an individual bird to explain how the head-tilting behavior functions. By focusing on events that take place during an animal's lifetime, this approach seeks to explain behaviors in terms of their immediate or **proximate causes**. In contrast, the second explanation addresses a "why" question about behavior: it examines the evolutionary and historical reasons for a particular behavior. By addressing previous events that influenced the features of an animal as we know it today, this approach seeks to explain behaviors in terms of their evolutionary or **ultimate causes**.

Although behavioral ecologists examine both proximate and ultimate causes in their research, they are primarily concerned with ultimate explanations of animal behaviors. We will follow their lead in this chapter, focusing on selected ultimate explanations for why animals behave as they do. We'll begin by examining how natural selection affects behavior.

Natural selection shapes animal behaviors over time

As we've seen in earlier chapters of this book, an individual's ability to survive and reproduce depends in part on its behavior. Therefore, natural selection should favor individuals whose behaviors make them efficient at activities such as foraging, obtaining mates, and avoiding predators.

To explore this idea further, recall from Concept 6.1 that natural selection is not a random process. Instead, when natural selection operates, individuals with particular traits consistently leave more offspring than do other individuals *because of* those traits. If the traits that confer advantage are heritable (i.e., determined in part by genes), then individuals that have those traits will tend to pass them to their offspring. In such cases, natural selection can cause **adaptive evolution**, a process in which traits that confer survival or reproductive advantages tend to increase in frequency over time.

Applying these ideas to heritable behaviors, we would predict that as an outcome of natural selection, individuals should exhibit behaviors that improve their chances of surviving and reproducing. As illustrated by the practice of infanticide by male lions—a behavior that increases a male's chance of reproducing before he is displaced by a younger male—animal behaviors are often consistent with this prediction. Further support comes from studies that have documented adaptive behavioral change as it took place.

For example, Silverman and Bieman (1993) reported an adaptive behavioral change in populations of the German cockroach (*Blattella germanica*) (**Figure 8.3**). In the 1980s, efforts to control this cockroach often used baits that combined an insecticide with a feeding stimulant, such as glucose. Initially, these baits were highly effective, killing the vast majority of the cockroaches that encountered them. Over time, however, a novel behavioral adaptation, glucose aversion, emerged in some cockroach populations. Cockroaches from these populations avoided feeding on glucose, causing the baits to become ineffective. This change in the feeding behavior of German cockroaches is heritable and is controlled by a single gene (Silverman and Bieman 1993). In particular, glucose aversion appears to result from mutations that affect taste receptor neurons. In individuals that exhibit glucose aversion, the presence of glucose activates taste receptor neurons that in other individuals are activated only by bitter substances (Wada-Katsumata et al. 2013).

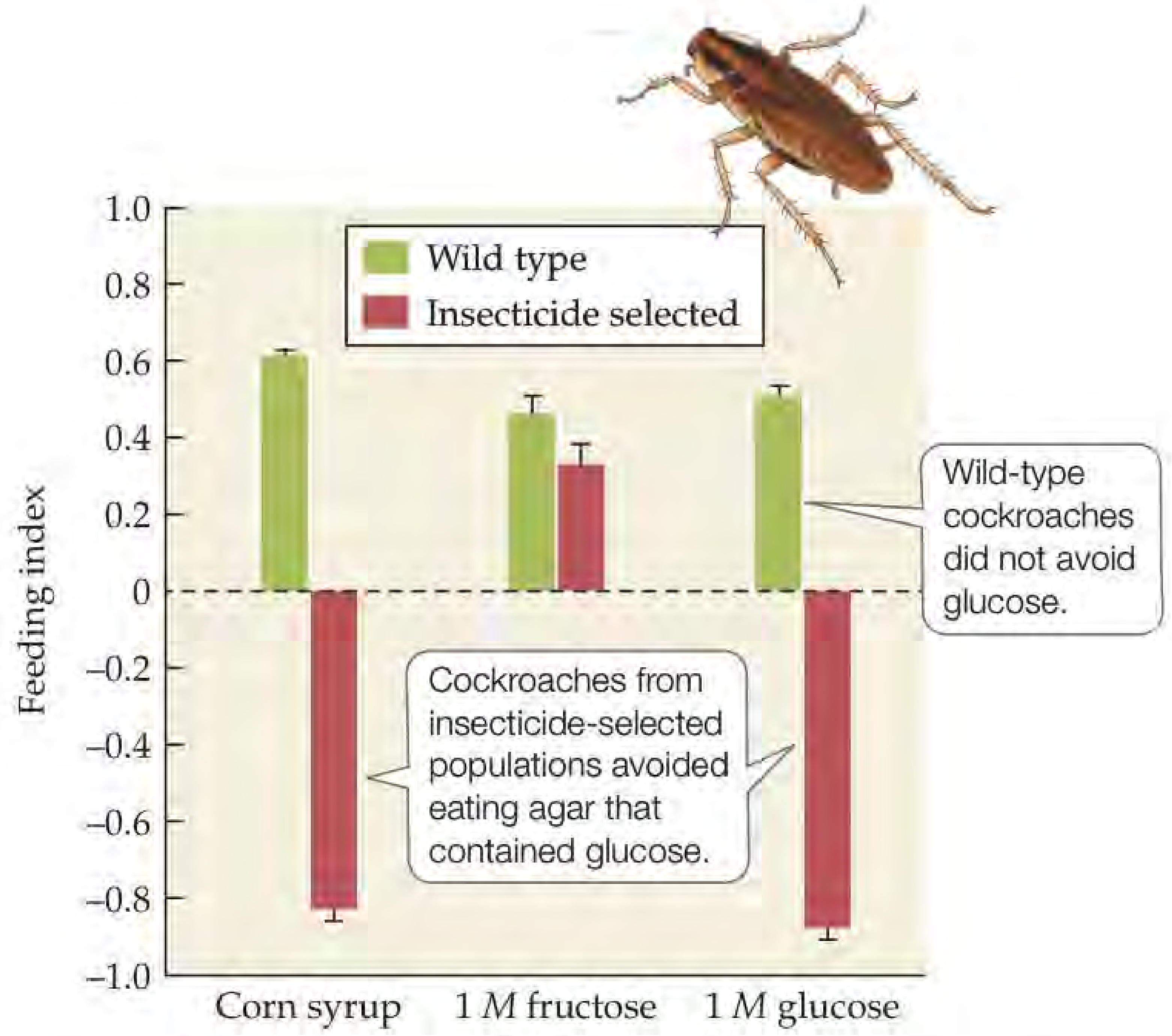


Figure 8.3 An Adaptive Behavioral Response Feeding behavior in two populations of the German cockroach (*Blattella germanica*), one of which (wild type) had no prior exposure to insecticides, while the other had been exposed to insecticides. Cockroaches could choose to eat plain (unsweetened) agar, agar that contained one of three sources of sugar—fructose, glucose, or corn syrup (which contains both fructose and glucose)—or both. The diets the cockroaches selected were characterized by a feeding index ranging from 1.0 (indicating that 100% of their diet consisted of agar containing glucose) to −1.0 (indicating that 100% of their diet consisted of plain agar). Error bars show one SE of the mean. (After Silverman and Bieman 1993.)

? Give both a proximate and an ultimate explanation for glucose aversion in *B. germanica.*

The increase in the frequency of glucose aversion in populations of cockroaches exposed to baits containing glucose shows how natural selection under different environmental conditions can shape behaviors over time. But for selection to have this effect—and for ultimate explanations of behavior to be convincing—a behavior must be determined at least in part by genes. Because later sections of this chapter emphasize ultimate explanations of behavior, we turn now to a closer examination of this key underlying assumption: that animal behaviors are determined by genes.

Behaviors are determined by genes and by environmental conditions

Many characteristics of an animal, including aspects of its behavior, are influenced both by genes and by environmental conditions (see Concepts 6.2 and 7.1). Later in this chapter, we'll discuss how certain features of the environment, such as the presence of predators, can alter an animal's behavior. Here we'll focus primarily on genes, but it is essential to bear in mind that environmental conditions also affect most behaviors, even those that are strongly influenced by genes.

The glucose aversion behavior of cockroaches that we have just discussed is heritable and appears to be controlled by a single gene. However, this behavior is a relatively simple one—a cockroach either avoids glucose or it does not. We might expect that such a specific and relatively simple behavioral choice could be controlled by one or a few genes. But what about more complex behaviors?

Weber et al. (2013) examined the genetics of one such behavior, burrow construction in mice. They studied two closely related species, oldfield mice (*Peromyscus polionotus*) and deer mice (*P. maniculatus*). In the wild, oldfield mice build complex burrows with a long entrance tunnel and an escape tunnel, while deer mice build much simpler burrows (**Figure 8.4**). Most other *Peromyscus* species construct simple burrows, or no burrows at all. The complex burrows built by oldfield mice are unique, and they may be an adaptation to living in open habitats that provide little protective cover: although snakes and other predators might spot oldfield mice easily in such habitats, the length of the burrow entrance tunnel and the presence of an escape tunnel might help a mouse evade a pursuing predator.

Weber and colleagues wanted to evaluate the contribution of genes to the unique burrowing behavior of oldfield mice. To do this, they took advantage of the facts that oldfield mice and deer mice can interbreed to form viable and fertile hybrid offspring (as can some other closely related species, such as wolves and coyotes) and that both species exhibit their usual burrowing behaviors in a laboratory enclosure. They examined the burrowing behaviors of oldfield mice, deer mice, and two different types of hybrid offspring: first-generation (F_1) hybrids (offspring of matings between oldfield mice and deer mice) and later-generation backcross hybrids (offspring of matings between F_1 individuals and deer mice).

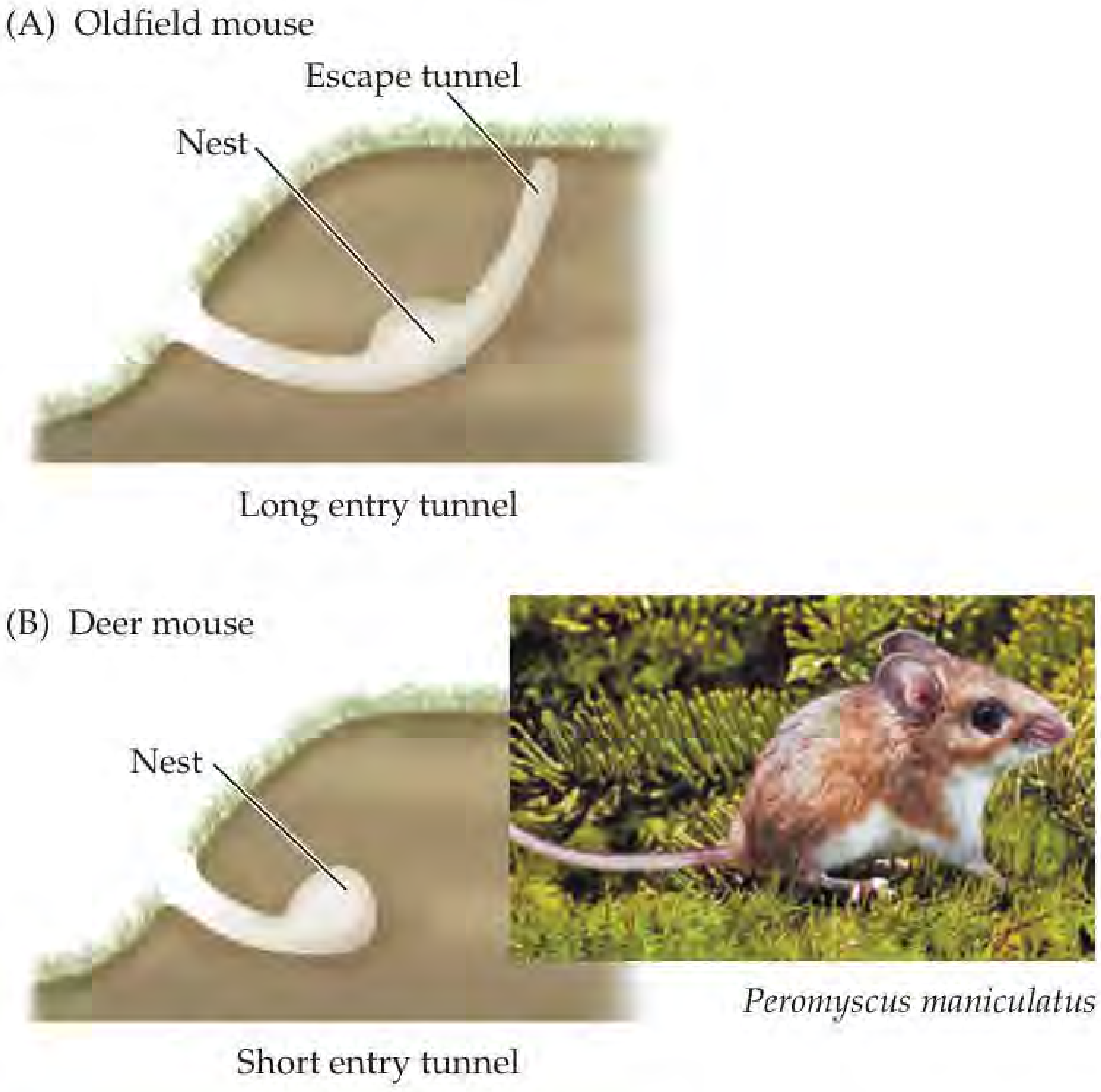


Figure 8.4 **Distinctive Mouse Burrows** (A) The oldfield mouse (*Peromyscus polionotus*) constructs a complex burrow with a long entrance tunnel and an escape tunnel. (B) The deer mouse (*P. maniculatus*) constructs a simpler burrow, with a short entrance tunnel and no escape tunnel.

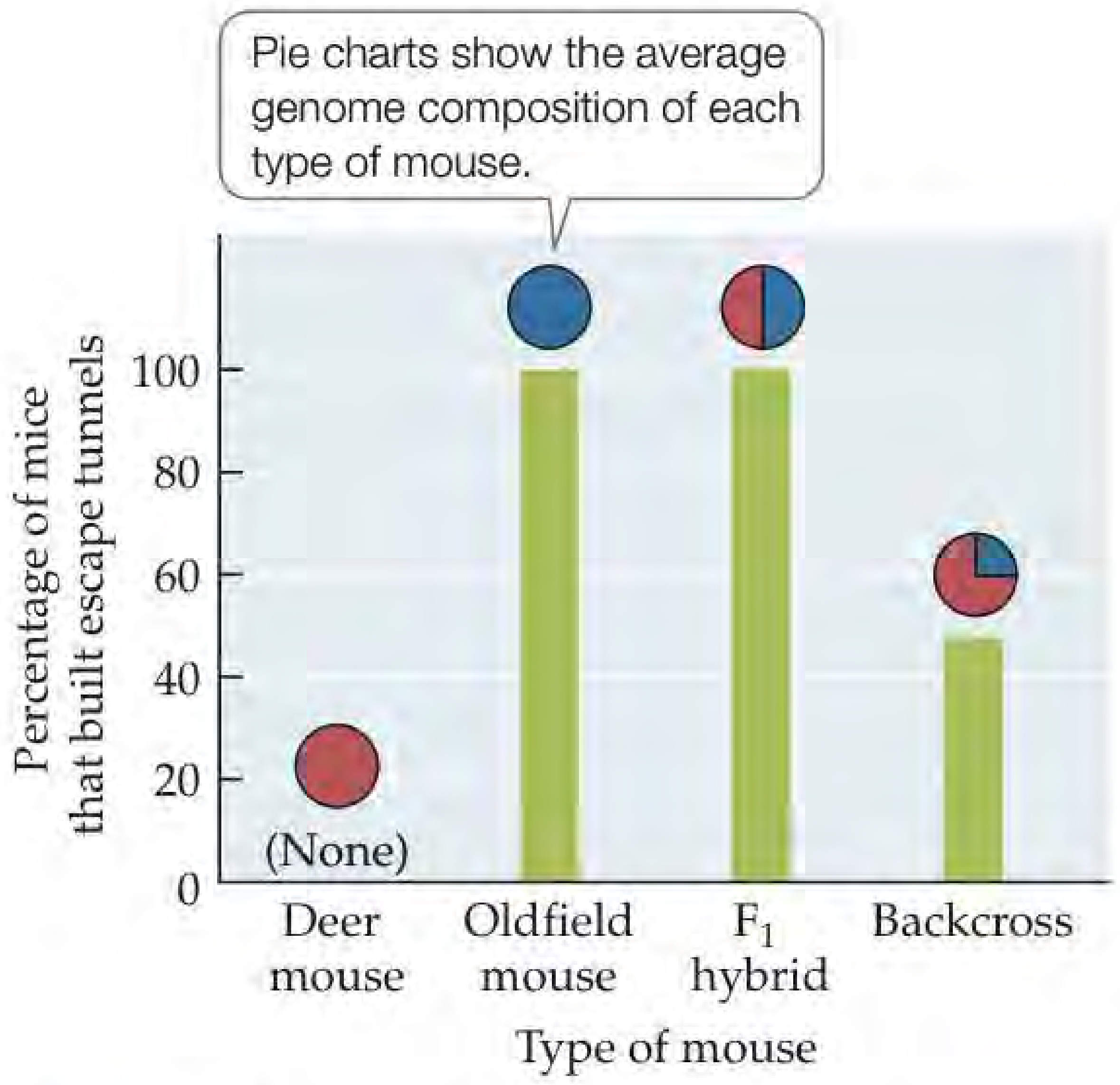

Pie charts show the average genome composition of each type of mouse.

Figure 8.5 **The Genetics of Escape Tunnel Construction** The graph shows the proportions of deer mice, oldfield mice, F_1 hybrids, and backcross mice (i.e., offspring of a hybrid mouse and a deer mouse) that constructed burrows with escape tunnels. (After Weber et al. 2013.)

? Do the colors shown in the pie charts match what you would expect based on the types of mice used in this study? Explain.

The results indicated that the complex burrowing behavior of oldfield mice is affected by several different DNA regions. As expected, all of the oldfield mice and none of the deer mice built escape tunnels. In addition, 100% of the F_1 hybrid mice built escape tunnels, and roughly 50% of the backcross mice built escape tunnels (**Figure 8.5**). These results are consistent with the building of escape tunnels being controlled by a single chromosomal location, or *genetic locus*. Further support for this conclusion was obtained using a genetic mapping approach called quantitative trait locus (QTL) analysis—Weber et al. found that building an escape tunnel was primarily determined by a single genetic locus. QTL analyses also showed that entrance tunnel length was affected by at least three separate genetic loci, all of which differed from the single locus that controlled escape tunnel construction. Thus, it appears that the complex burrow-building behavior of oldfield mice evolved as a combination of two simpler behaviors (construction of long entrance tunnels and escape tunnel construction), each of which was affected by a different set of genetic instructions.

The study by Weber et al. is unusual in its use of both behavioral observations and genetic mapping to examine how genes affect a complex behavior of ecological importance. Although relatively few studies have identified genes that affect other such behaviors, a wide range of behaviors are known to be heritable, and typically those behaviors are influenced by multiple genes (van Oers and Sinn 2013).

Overall, it is clear that genes affect many behaviors, but it is important to keep a few caveats in mind. In particular, it is usually a mistake to assume that behaviors are under the control of one or a few genes. It is also wrong to assume that an individual that has an allele associated with a certain behavior will always perform that behavior—like an inflexible, lumbering robot under the strict control of its genes. Instead, two individuals with identical alleles may behave differently. Moreover, as we'll discuss below, individuals often change their behavior when in different environments. Nevertheless, by assuming that genes affect behaviors and that natural selection has molded behaviors over time, we can make specific predictions about how animals will behave in particular situations. Even when these predictions turn out to be wrong, an evolutionary view of behavior provides a productive approach to the study of animal behavior that can help us understand how animals interact in nature.

CONCEPT 8.2

Animals make behavioral choices that enhance their energy gain and reduce their risk of becoming prey.

Foraging Behavior

As we've seen, the fact that there are costs and benefits to the behavioral choices that animals make suggests that their behaviors have been shaped by natural selection over time. In this section, we'll consider this line of reasoning in more detail, focusing on one of the central activities of all animals: obtaining food.

Optimal foraging theory addresses behavioral choices that enhance the rate of energy gain

The availability of food varies greatly over space and time. For example, some areas of a landscape may have a higher density of prey or host individuals than others due to differences in water or nutrient availability associated with differences in local conditions. In addition, some food items may be easier to obtain than others because of factors other than abundance, including how easy they are to detect, capture, or subdue.

If energy is in short supply, then animals moving through a heterogeneous landscape should invest the majority of their time in acquiring the highest-quality food resources possible in places where they are most abundant and that are the shortest distance away. Such behavior should maximize the amount of energy obtained per unit of feeding time and minimize the risks involved, such as that of becoming food for another animal. These ideas are the essence of the theory of **optimal foraging**, which proposes that animals will maximize the amount of energy acquired per unit of feeding time. Optimal foraging theory relies on the assumption that natural selection acts on the foraging behavior of animals to maximize their rate of energy gain.

According to one formulation of optimal foraging theory, the profitability of a food item to a foraging animal depends on the net amount of energy it gets from the food relative to the amount of time it spends obtaining and processing the food, or, in mathematical terms,

$$P = \frac{E}{t}$$

where P is profitability, E is the net energy value of the food, and t is the time invested in obtaining and processing the food. The net energy value is the energy gained minus the energy invested in obtaining and processing the food. If an animal is foraging optimally and has a choice between two equally abundant food items, it will select the food with the higher P.

Another way to consider foraging decisions is to represent the energetic consequences of foraging behavior with a simple conceptual model that describes the net amount of energy that an animal gets from its food (**Figure 8.6**). At first, the total amount of energy that an animal obtains from its food (blue curve) increases rapidly with the effort it invests—that is, with the time and energy it spends searching for, capturing, subduing, and consuming food. At some point, however, a further increase in foraging effort provides relatively little additional energy, and the net energy gain begins to decrease. Several factors may cause this decrease, including a limitation on how much food the animal can carry or ingest.

While the models discussed here are simple, they provide a basis for making quantitative predictions about animal foraging behavior. More sophisticated models have been used to derive hypotheses that can be tested under field or laboratory conditions. An important component of these models is the currency (such as net energy gain) that is used to determine the benefit. Such models might incorporate, for example, net energy gained, time spent feeding, and risk of predation (Schoener 1971). If foraging behavior is an adaptation to limited food supplies, then we must be able to relate the benefit of that behavior to the survival and reproduction of the animal.

TESTS OF OPTIMAL FORAGING THEORY Research addressing optimal foraging has focused on diet selection, selection of patches to feed in, time spent in food patches, and prey movements (Pyke et al. 1977). John Krebs

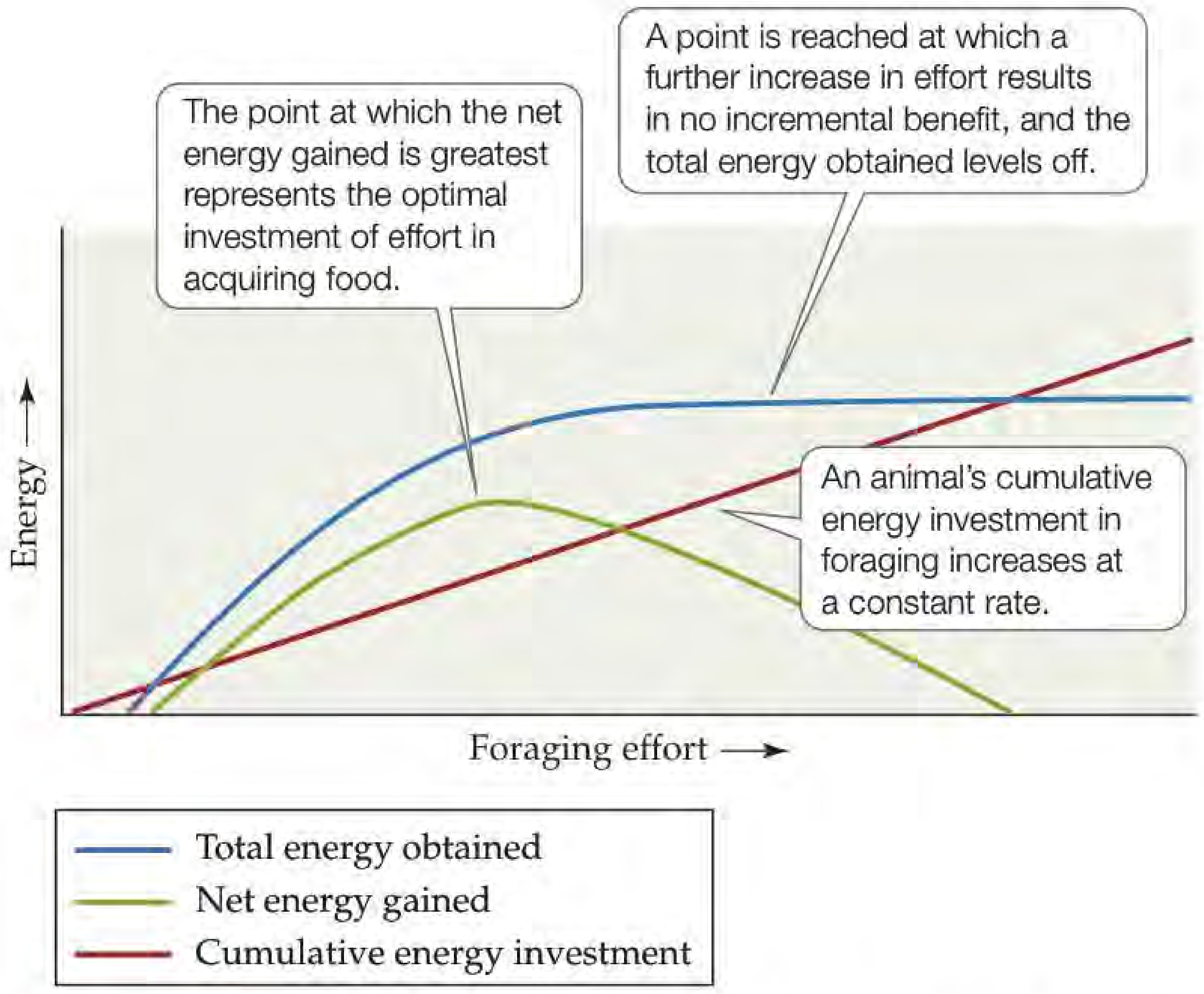


Figure 8.6 Conceptual Model of Optimal Foraging The net energy gained from foraging (green curve) equals the total energy obtained from the food acquired (blue curve) minus the cumulative energy invested in acquiring that food (red curve). This simple model can be used to test whether animals forage in a manner that results in the maximum benefit, based on estimates for the total energy obtained and the cumulative energy invested.

? Suppose you could estimate the net energy gained at different levels of foraging effort expended by lizards eating ants in the desert. How could you use that information to test whether the lizards foraged optimally?

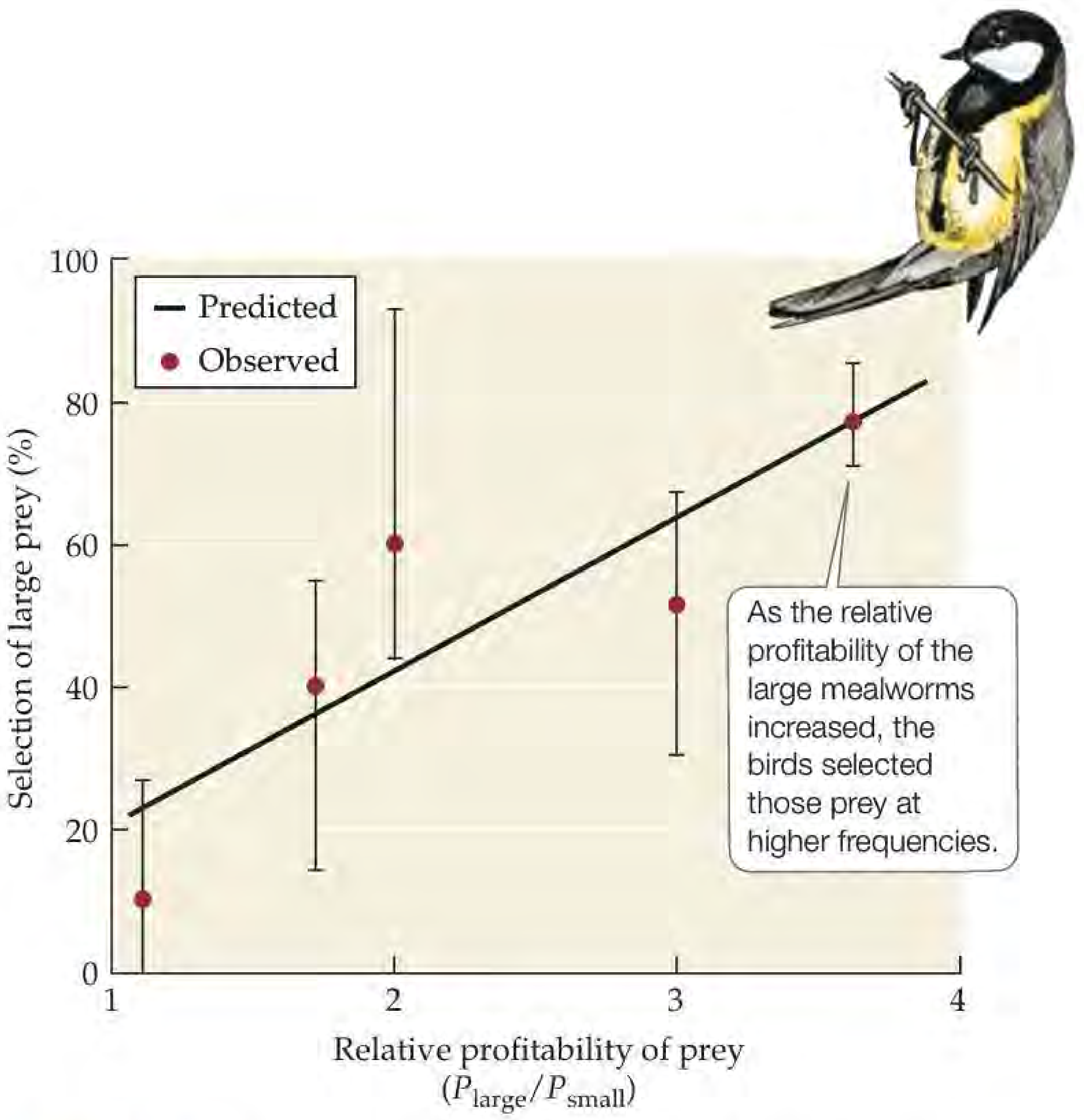
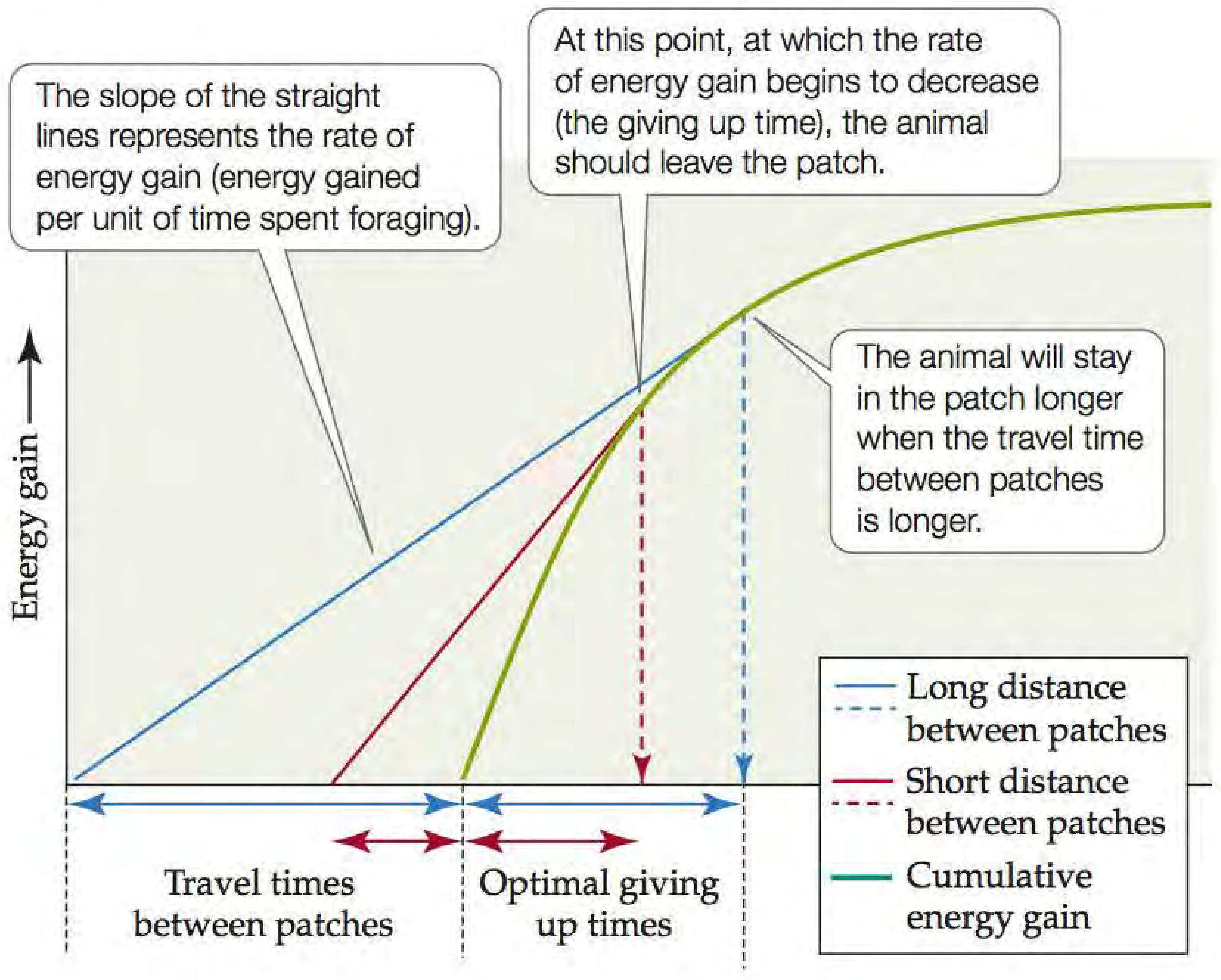


Figure 8.7 Effect of Profitability on Food Selection Krebs and colleagues used an optimal diet selection model, along with measurements of prey handling time for individual birds, to predict the rate at which great tits (*Parus major*) would select large over small mealworms as their encounter rates with the two prey types were varied (expressed as the calculated ratio of profitabilities of the prey types). Error bars show ± one SE of the mean. (After Krebs et al. 1977.)

and colleagues (1977) devised a unique way to evaluate whether great tits (*Parus major*), a common bird found throughout much of Eurasia and northern Africa, selected prey types of greatest profitability. They placed captive birds next to a moving conveyer belt carrying prey that differed in size (large and small mealworms) and in the time required to obtain them (each of the small mealworms was taped to the surface of the conveyer belt). By changing the proportions of the prey types and the distances between adjacent prey on the conveyer belt (*encounter rates*), the researchers varied the profitability of the large and small mealworms. Using a model of optimal foraging and measurements of the times it took individual birds to subdue and consume the prey (*handling time*), they predicted how frequently the birds should select the large mealworms as encounter rates with the two prey types were varied. The birds consumed an increasing percentage of large mealworms as the relative profitability of those larger prey increased (**Figure 8.7**), just as the model predicted.

In a field study focusing on diet selection, the forager under study was the Eurasian oystercatcher (*Haematopus ostralegus*), a shorebird that eats bivalves (e.g., clams and mussels). Oystercatchers must find a bivalve buried in the sand, lift it out, and open it before they can eat it. For bivalves below a certain size, the net energy gain from this effort is small, setting a lower limit on the bivalve size selected by the oystercatchers. Bivalves above a certain size have thicker shells and require more effort to open, setting an upper limit on the bivalve size selected by the birds. Meire and Ervynck (1986) demonstrated that oystercatchers select prey of sizes that fall between these limits, which provide the most energy gain for the effort, despite the relatively low abundance of prey of these sizes.

THE MARGINAL VALUE THEOREM Another aspect of optimal foraging theory considers the habitat in which an animal forages as a heterogeneous landscape made up of patches containing different amounts of food. To optimize its energy gain, an animal should forage in the most profitable patches—those in which it can achieve the highest energy gain per unit of time. We can also consider the benefit obtained by a foraging animal from the perspective of time spent in a patch. Once the forager finds a profitable patch, its rate of energy gain is initially high, but that rate



The slope of the straight lines represents the rate of energy gain (energy gained per unit of time spent foraging).

At this point, at which the rate of energy gain begins to decrease (the giving up time), the animal should leave the patch.

The animal will stay in the patch longer when the travel time between patches is longer.

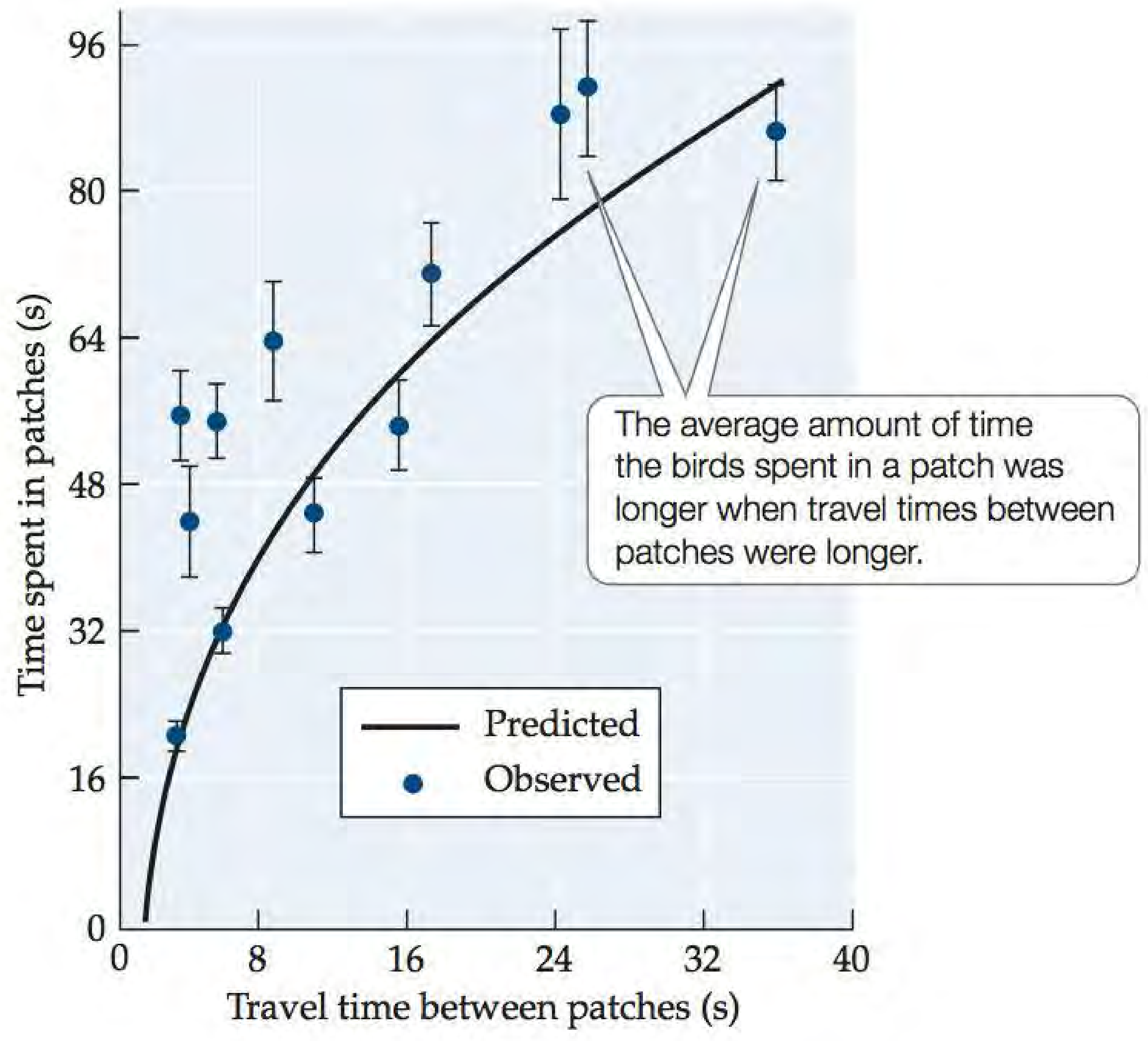
Figure 8.8 The Marginal Value Theorem The marginal value theorem assumes that a foraging animal will encounter patches containing varying amounts of food. The animal's rate of energy gain in a patch (energy gained per unit of time spent foraging) is initially high but decreases as the animal depletes the food supply in the patch. The time the animal spends in a patch should optimize its rate of energy gain.

? If prey density or prey quality is low, and the cumulative energy gain therefore levels off at a lower level, how will this influence the giving up time?

decreases and eventually becomes marginal as the forager depletes the food supply (**Figure 8.8**). A foraging animal should stay in a patch until the time when the rate of energy gain in that patch has declined to the average rate for the habitat (known as the *giving up time*), then depart for another patch. The giving up time should also be influenced by the distance to other patches. Effort must be invested in traveling to another patch, so the animal may accept a lower rate of energy gain if the distance between patches is greater. This conceptual model, called the **marginal value theorem**, was initially developed by Eric Charnov (1976). It can be used to evaluate the influences of distance between patches, the quality of the food in a patch, and the animal's energy extraction efficiency on the giving up time. The model has also been extended to other "giving up" problems in behavioral ecology, including how long to copulate and when to cease guarding a nest and seek other mates.

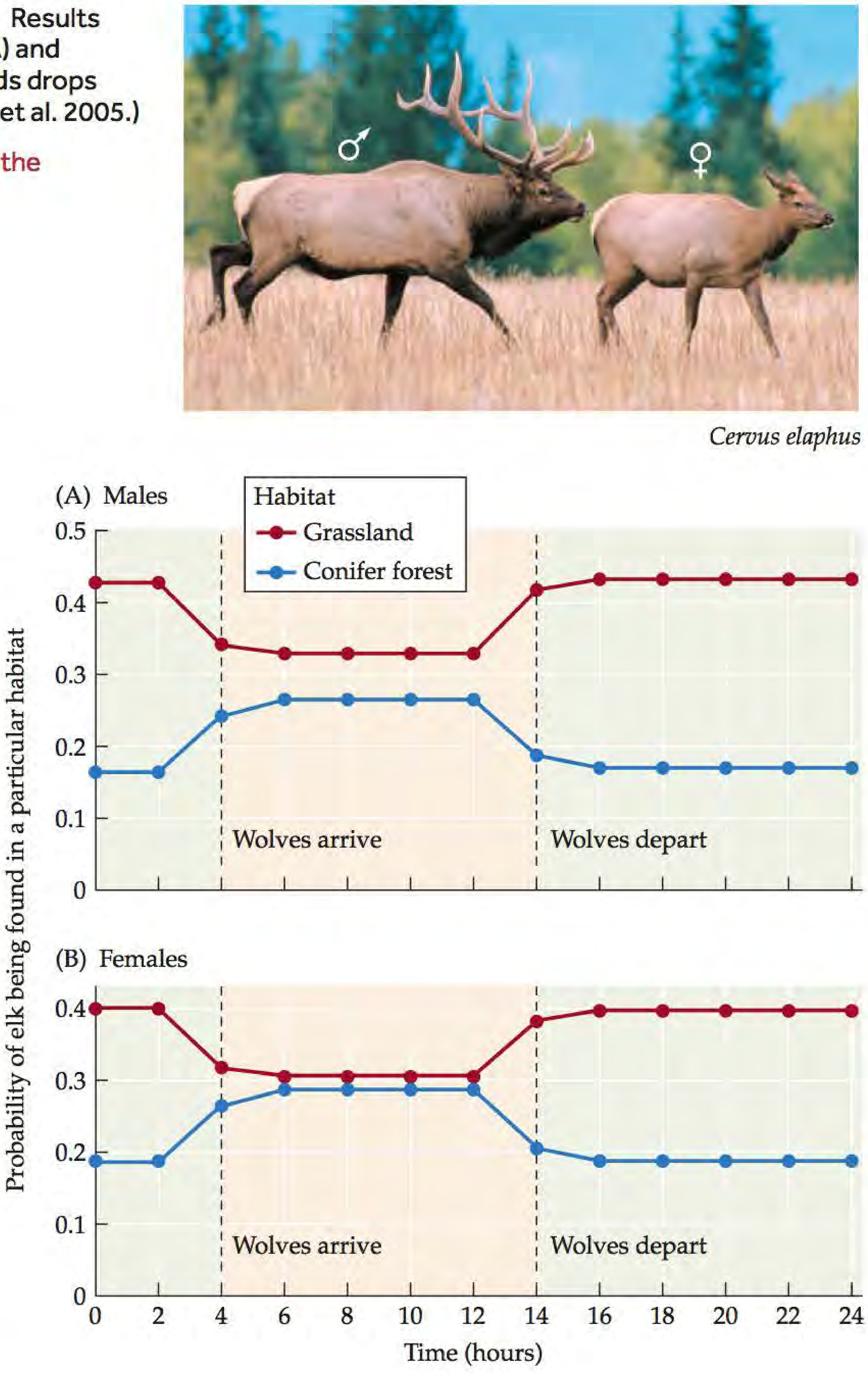
One of the predictions of the marginal value theorem is that the longer the travel time between food patches, the longer an animal should spend in a patch (see Figure 8.8). This prediction was tested by Richard Cowie (1977) using a laboratory setup with great tits in a "forest" composed of wooden dowels. The food "patches" consisted of sawdust-filled plastic cups containing mealworms. The "travel time" among patches was manipulated by placing cardboard covers on top of the food cups and adjusting the ease with which they could be removed by the birds. Cowie used the marginal value theorem to predict the amount of time the birds should spend in the patches, based on the travel time between them. His results matched his predictions fairly well (Cowie 1977) (**Figure 8.9**). Similar results have been obtained from other laboratory experiments as well as from studies in natural settings, such as James Munger's 1984 study on the behavior of horned lizards (*Phrynosoma* spp.) foraging for ants in the Chihuahuan Desert.

While evidence supports some aspects of optimal foraging theory, significant criticisms have been leveled at it as well. Optimal foraging theory best describes the foraging behavior of animals that feed on immobile prey and applies less well to animals feeding on mobile prey (Sih and Christensen 2001). In addition, the assumptions that energy is always in short supply and that a shortage of energy dictates foraging behavior may not always be correct. Carnivores, in particular, may not lack for food resources to the degree assumed in optimal foraging models (Jeschke 2007). Furthermore, resources other than energy may be involved in the selection of food items, particularly nutrients such as nitrogen and sodium. And as we'll see next, additional considerations for foragers include the risk of predation and the defenses of prey.



The average amount of time the birds spent in a patch was longer when travel times between patches were longer.

Figure 8.9 Effect of Travel Time between Patches In a laboratory experiment, Cowie used the marginal value theorem to predict how the travel time between patches would affect the average amount of time great tits (*Parus major*) spent in a patch. Error bars show ± one SE of the mean. (After Cowie 1977.)



Cervus elaphus

Figure 8.10 Movement Responses of Male and Female Elk Results from a statistical analysis of daily movement patterns of male (A) and female (B) elk show that the probability of finding elk in grasslands drops when wolves arrive, then rises when wolves depart. (After Creel et al. 2005.)

? Compare and contrast how male and female elk respond to the presence of wolves.

Individuals often alter their foraging decisions when predators are present

While the intake of food is important to an animal, what really matters from an evolutionary perspective is its production of offspring. An individual that is well fed but does not survive long enough to reproduce will not pass its genes to future generations. As this observation suggests, a forager may face trade-offs in which achieving one objective (such as eating) comes at the expense of another (survival). Trade-offs that affect foraging decisions may be related to predators (an herbivore may avoid an area with ample food if predators are present), environmental conditions (in the desert, a foraging animal may retreat to a burrow or shade when temperatures become too hot), or physiological conditions (a hungry animal may tolerate greater risks when foraging than will a well-fed animal). Our focus here will be on how predators affect foraging decisions.

For example, Creel and colleagues (2005) studied how the presence of wolves affected the foraging behavior of elk (*Cervus elaphus*) in the Greater Yellowstone Ecosystem. The researchers used GPS radio collars to track the daily movements of elk. On days when wolves were known to be present in the area, elk moved into wooded regions, which offered more protective cover, but less food, than the grasslands where the elk preferred to forage but where they were more vulnerable to wolf predation. Results from a statistical analysis of elk movements provided additional evidence that elk moved into forests when wolves arrived and returned to grasslands when wolves departed (**Figure 8.10**).

Similar results have been found in aquatic environments. For example, Werner et al. (1983) examined how predators affect the foraging decisions of the bluegill sunfish (*Lepomis macrochirus*). Identical sets of sunfish in three size classes (small, medium, and large) were introduced on both sides of a divided pond; a predatory fish, the largemouth bass (*Micropterus salmoides*), was also introduced on one side of the pond. The sizes of sunfish and bass were selected such that sunfish in the smallest size class would be very vulnerable to the bass predators, while sunfish in the largest size class were too large for the bass to eat. Sunfish in the larger two size classes foraged in similar ways on both sides of the pond, with their habitat choice and diet matching predictions based on optimal foraging theory; the same was true for the small sunfish on the half of the pond lacking predators. In the presence of predators, however, the small individuals increased the time they spent foraging in vegetation, a habitat that provided greater cover from largemouth bass but only one-third the rate of food intake available in more open habitats.

Researchers have also tested whether a perceived risk of predation can alter foraging patterns, even in the absence of actual predation. In one such study, Zanette et al. (2011) exposed the nests of some song sparrows (*Melospiza melodia*) to recordings of calls and sounds from their predators (such as raccoons, ravens, or hawks), while other nests were exposed to recordings of calls and sounds from nonpredators (such as seals or geese). The researchers had protected all the nests from actual predators with electric

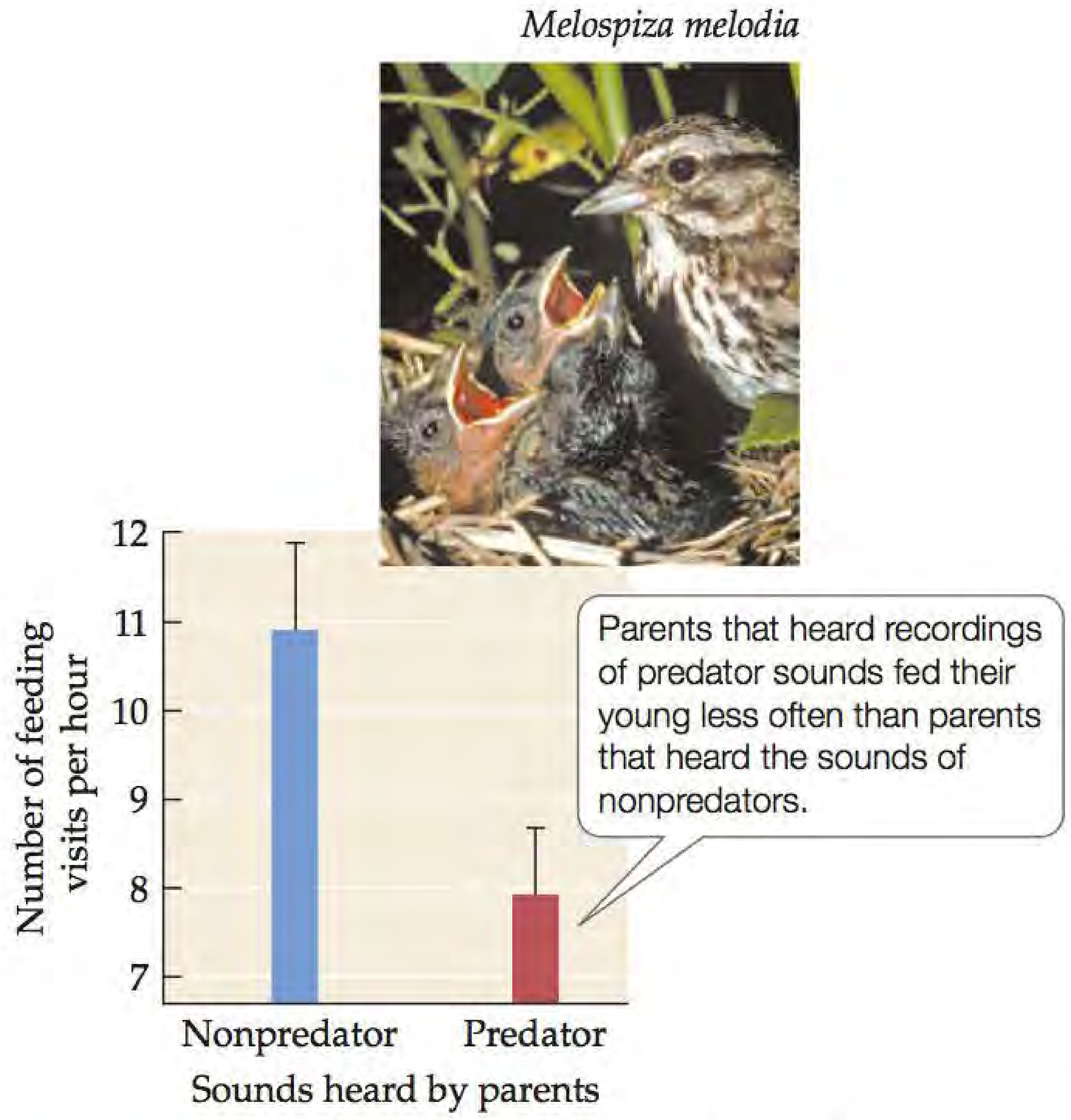


Figure 8.11 Young Receive Less Food When Parents Fear Predators The number of times per hour that song sparrow parents feed their offspring drops when the parents are exposed to recordings of sounds made by predators. Error bars show one SE of the mean. (After Zanette et al. 2011.)

fencing and netting (the netting and other aspects of this experiment are described in more detail in **Web Extension 8.2**). Song sparrows exposed to recordings of predators fed their young fewer times per hour than did sparrows that heard recordings of nonpredators (**Figure 8.11**); song sparrows that heard predators also built their nests in denser, thornier vegetation and spent less time incubating their eggs than did sparrows exposed to recordings of nonpredators. We'll explore the consequences of such behavioral changes in Connections in Nature at the end of this chapter.

The song sparrow, elk, and sunfish examples are representative of hundreds of other studies showing that prey alter their foraging behavior in the presence of predators (Lima 1998; Verdolin 2006). As we'll see next, when predators are present, prey make other behavioral changes that can reduce their chance of being eaten.

Prey exhibit behaviors that can prevent detection or deter predators

Predators can kill large numbers of prey, exerting strong selection on prey populations. As a result of such selection pressures, prey species have evolved a broad range of defenses against their predators. We'll focus here on antipredator behaviors; in Concept 13.2, we'll discuss other forms of defense, including physical defenses, toxins, and morphological forms of camouflage.

Antipredator behaviors include those that can help prey avoid being seen, detect predators, prevent attack, or escape once attacked (**Figure 8.12**). Behaviors that can help prey avoid being seen include hiding, remaining still when predators are nearby, and performing risky activities (such as foraging) during times of day when predators are not active. Other animals make themselves difficult to see by covering their bodies with material that blends into their environment, such as portions of flower petals (in some caterpillars) or feces (some beetle larvae; see Figure 8.12A). With respect to detecting predators, prey often remain highly vigilant for predators, and some birds, lizards, and mammals can remain alert even while sleeping (see Figure 8.12B). There is also a wide variety of ways that prey seek to prevent attack once they are seen. For example, juvenile decorator crabs (*Libinia dubia*) attach to their bodies bits of an alga that local fishes find unpalatable, an action that was found to increase their rate of survival (Stachowicz and Hay 1999); older crabs, which are too large for the fish to eat, do not engage in this behavior. When threatened, some prey make sudden movements or place their body in positions that may startle a predator, as illustrated by the display of the mantis in Figure 8.12C. Some prey send predators a signal, in effect conveying, "I see you, I'm faster than you, so don't bother to attack me." The stotting behavior of antelopes (see Figure 8.12D) is thought to be one such signal. Other examples of prey signaling to prevent attack include lizards that perform "push-ups" (indicating their overall physical condition) and ground squirrels that deliberately approach rattlesnakes, often within striking distance, while waving their tails from side to side (tail-flagging). Tail-flagging was found to be effective: it deterred rattlesnakes from striking, and it increased the chance that a snake would abandon its ambush site (Barbour and Clark 2012).

If a predator attacks and captures (or is about to capture) its prey, the potential victim may resort to extreme behaviors. A hognose snake, for example, may play dead when captured, extruding its tongue and emitting a foul odor that resembles the smell of decaying meat, all the while keeping a close eye on its attacker (see Figure 8.12E). This behavior may work because many predators will not eat carrion. As a last resort, many prey defecate, urinate, or extrude other unpleasant substances, such as the large amounts of mucus secreted by a hagfish under attack (this mucus sometimes suffocates the predator). Other species detach parts of the body when threatened or grabbed. A gecko, for example, can drop its tail, which wriggles on the ground, distracting the predator. Some sea cucumbers take such evasive maneuvers to a unique level: when captured, they turn themselves partially inside out, startling the attacker and covering it with a tangled mass of internal organs. The sea cucumber then detaches those organs

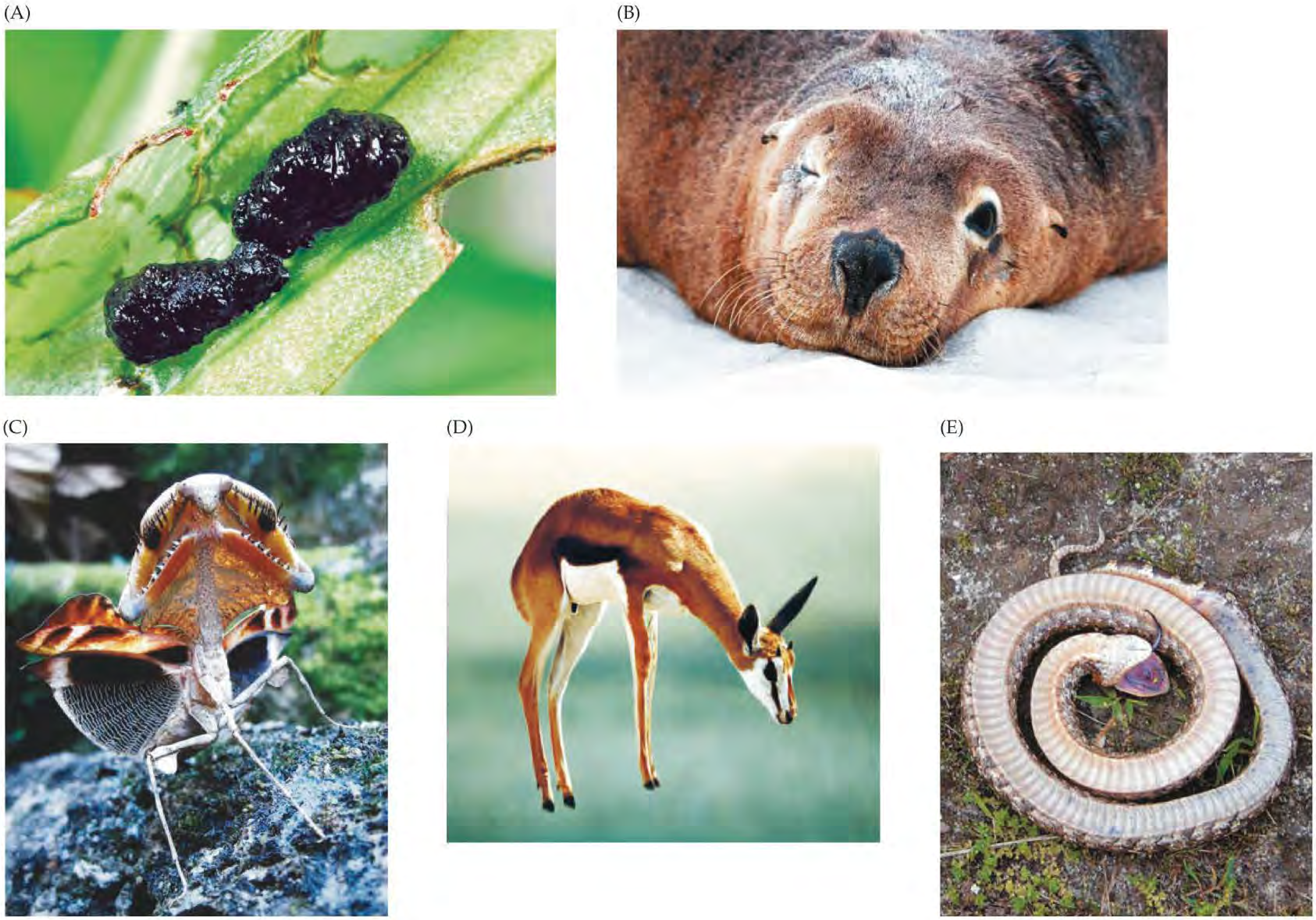


Figure 8.12 **Examples of Antipredator Behaviors**
(A) Larvae of the lily beetle (*Liloceris lilii*) cover themselves with their own feces, making them unpalatable to predators. (B) Australian sea lions (*Neophoca cinerea*) can literally sleep with one eye open, with half their brain in a state of sleep while the other half remains alert for danger. (C) When threatened, the praying mantis (*Deroplatys*) rears up and configures its body as shown, a sudden transformation that can startle predators. (D) A springbok (*Antidorcas marsupialis*) displays a stiff-legged jumping behavior known as stotting or pronking, which is thought to discourage predators from pursuing the small gazelle. (E) When captured, hognose snakes such as this eastern hognose snake (*Heterodon platirhinos*) play dead and emit an odor that smells like decaying meat; this behavior can deter predators that will not eat carrion. (C courtesy of James O'Hanlon.)

and swims away; later, it regrows the missing organs in a remarkable example of self-regeneration.

Having examined the foraging and antipredator behaviors of animals from an evolutionary perspective, we turn now to another key animal activity: sex.

CONCEPT 8.3

Mating behaviors reflect the costs and benefits of parental investment and mate defense.

Mating Behavior

Males and females differ in their sexual organs and in other ways that are directly related to reproduction. But there are other, more puzzling differences between them. Males are often larger or more brightly colored than females, they may possess unusual weapons (such as large horns), or they may have gaudy ornaments, such as the extravagant plumage of a male Argus pheasant (*Argusianus argus*) or a male peacock (**Figure 8.13**). In addition, males and females often differ in their mating behavior. In many species, the males may fight, sing loudly, or

Figure 8.13 A Male Shows Off The Indian peafowl (*Pavo cristatus*) is native to the forests of India and Sri Lanka in South Asia. The males, or peacocks, display their remarkable tail feathers as they attempt to attract and mate with the smaller, duller females (peahens).

Figure 8.14 A Male Courtship Dance Male blue-footed boobies (*Sula nebouxii*) of the Galápagos flaunt their blue feet and perform a strutting dance to impress and gain access to females. Part of this courtship display includes the "sky-pointing" behavior seen here.

perform strange antics to gain access to females (**Figure 8.14**). Furthermore, males may be willing to mate with any female who will have them. Females, on the other hand, rarely attempt to court males and typically are more choosy about who they will mate with. What causes such differences between the sexes?

Differences between males and females can result from sexual selection

Charles Darwin (1859, 1871) concluded that the often extravagant features of males did not provide a general advantage to members of a species, reasoning that if they did, both sexes would have them. He proposed instead that such features resulted from **sexual selection**, a process in which individuals with certain characteristics gain an advantage over others of the same sex *solely with respect to mating success*. We'll focus initially on sexual selection among males.

EVIDENCE FOR SEXUAL SELECTION Darwin pointed out that when individuals compete against others of their sex for mates, they typically use either force or charm. A male lion, for example, tries to repel his rivals by force, while a male pheasant or peacock tries to attract females to him (and away from other males) by displaying his beautiful tail feathers.

In species in which males fight over the right to mate with females, Darwin (1871) argued, the large size, strength, or special weapons of such males could have evolved by sexual selection. To make his case, Darwin began by pointing out that males often fought ferociously over females. He then described how males with the largest size, strength, and weaponry typically won such battles and therefore sired more offspring than other males. The large size, strength, or weaponry of the victors would then be passed on to their male descendants—causing these traits to become increasingly common over time. Modern studies corroborate Darwin's argument. For example, in bighorn sheep, large rams with a full curl of horns typically defeat other males in battles over the right to mate with females and therefore sire more offspring than other rams (see the Case Study in Chapter 6). Since body size and horn size are heritable traits (Coltman et al. 2003), the male offspring of the victors also tend to be large and strong, with a full curl of horns; over time, this process causes the large size of males and their full curl of horns to become common.

Darwin also thought that extravagant traits used by males to charm females (and not used in fighting) could have arisen by sexual selection. For example, he wrote of his "conviction that the male Argus pheasant acquired his beauty gradually, through the preference of the females during many generations for the more highly ornamented males." But Darwin's hypothesis that female mating preferences could lead to the evolution of more highly ornamented or brightly colored males was tested by few researchers prior to Malte Andersson's classic 1982 study on the long-tailed widowbird (*Euplectes progne*).

Male long-tailed widowbirds are mostly black and have extremely long tail feathers, the longest of which reach 50 cm. In contrast, females are mottled brown and have short tails (ca. 7 cm). Like many other animals, male widowbirds establish **territories**, areas that they defend against intruders. In the grasslands of Kenya, where Andersson studied

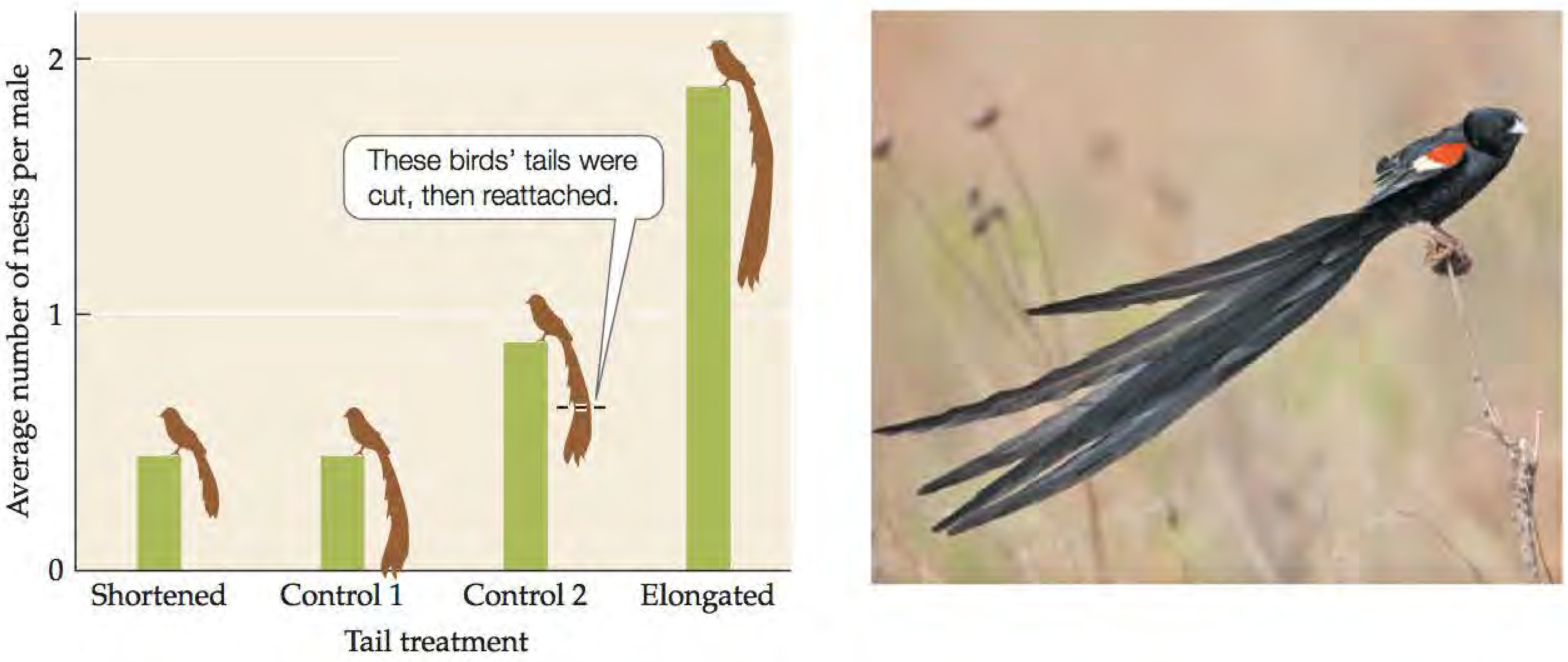


Figure 8.15 Males with Long Tails Get the Most Mates The mating success of male long-tailed widowbirds (*Euplectes progne*) depends on the length of their tails, as Malte Andersson discovered by experimentally altering the tails of wild birds. (After Andersson 1982.)

? Explain why Malte Andersson used the two types of controls described in the text.

these birds, male widowbirds establish and defend territories in which females can feed and build their nests.

To test whether female mating preferences could have driven the evolution of the long tails found in males, Andersson captured birds and subjected them to four treatments: (1) a control treatment in which the tails of the birds were not altered; (2) a second control treatment, in which the birds' tails were first cut at the midpoint and then glued back on; (3) a treatment in which the birds' tail lengths were shortened (cut to ca. 14 cm); and (4) a treatment in which the birds' tail lengths were increased (feathers cut from birds in treatment III were glued to the tails of these birds).

Andersson found that males with lengthened tails had higher mating success than control males or males with shortened tails (**Figure 8.15**). There were no differences among treatments in the courtship behavior of the males or the vigor with which they defended their territories. Overall, Andersson's results support the hypothesis that female mating preferences affect male mating success and hence may have selected for the extremely long tails of male widowbirds. Many other studies since have found similar results.

BENEFITS TO CHOOSY FEMALES In some species, a male that attempts to charm a choosy female into mating with him may provide direct benefits to the female, such as gifts of food, help in rearing the young, or access to a territory that has good nesting sites, abundant food, or few predators. But in other species, once a male has wooed a choosy female, he provides his sperm and little else. In cases in which few or no direct benefits are provided, why do females prefer to mate with males that have certain features (such as an elaborate ornament or a loud mating call)?

Current hypotheses propose that the female receives indirect genetic benefits when she chooses such males. For example, according to the *handicap hypothesis*, a male that can support a costly and unwieldy ornament, such as an extremely long tail, is likely to be a vigorous individual whose overall genetic quality is high. The idea here is that the male's ornament signals to females, "Look at me, I'm dragging this stupid tail around but I'm still alive, so you know I must have great genes! Come and mate with me." A female that mates with such a male benefits (indirectly) because both her sons and her daughters will inherit good genes from the male. As a result, her offspring will tend to survive or reproduce better than they would have had she selected another male as her mate. Alternatively, genetic benefits may come from the same genes that made the male attractive in the first place. According to this idea, sometimes called the *sexy son hypothesis*, the female receives indirect genetic benefits through her sons, who will themselves be attractive to females and produce many grandchildren.

Wilkinson and Reillo (1994) tested these hypotheses with a study of the stalk-eyed fly *Cyrtodiopsis dalmanni*. The eyes of this fly are positioned at the ends of long, thin stalks; the males in particular have extremely long eyestalks (**Figure 8.16**).

Figure 8.16 The Bizarre Eyes of a Stalk-Eyed Fly The eye span of a male stalk-eyed fly (*Cyrtodiopsis dalmanni*) can exceed the length of its body. (Courtesy of Gerald S. Wilkinson.)

What maintains these bizarre-looking appendages? Eyestalk length is heritable, and field studies show that females prefer to mate with males that have the longest eyestalks. The researchers established three laboratory populations of these flies, which they studied for 13 generations. In each generation, they allowed only some of the flies to mate and produce offspring. In the control population, in each generation, 10 males and 25 females were selected at random as breeders. In the "long-selected" population, the breeders were the 10 males with the longest eyestalks (of 50 males selected at random) and 25 females selected at random. Finally, in the "short-selected" population, the breeders were the 10 males with the shortest eyestalks (of 50 males selected at random) and 25 females selected at random.

After 13 generations, flies in the short-selected population had substantially shorter eyestalks than did flies in the other two populations. In addition, the mating preferences of females differed among the populations: when given a choice in a separate experiment, females from the short-selected population preferred males with short eyestalks, while females from the control and long-selected populations preferred males with long eyestalks (**Figure 8.17**). This result indicates that selection on one trait (eyestalk length in males) also caused the evolution of a different trait (female mating preference). Such evolutionary changes have the potential to be self-reinforcing. For example, when females selected males with long eyestalks as their mates, their male offspring would have longer eyestalks than their fathers and their female offspring would show stronger preference for long eyestalks than their mothers.

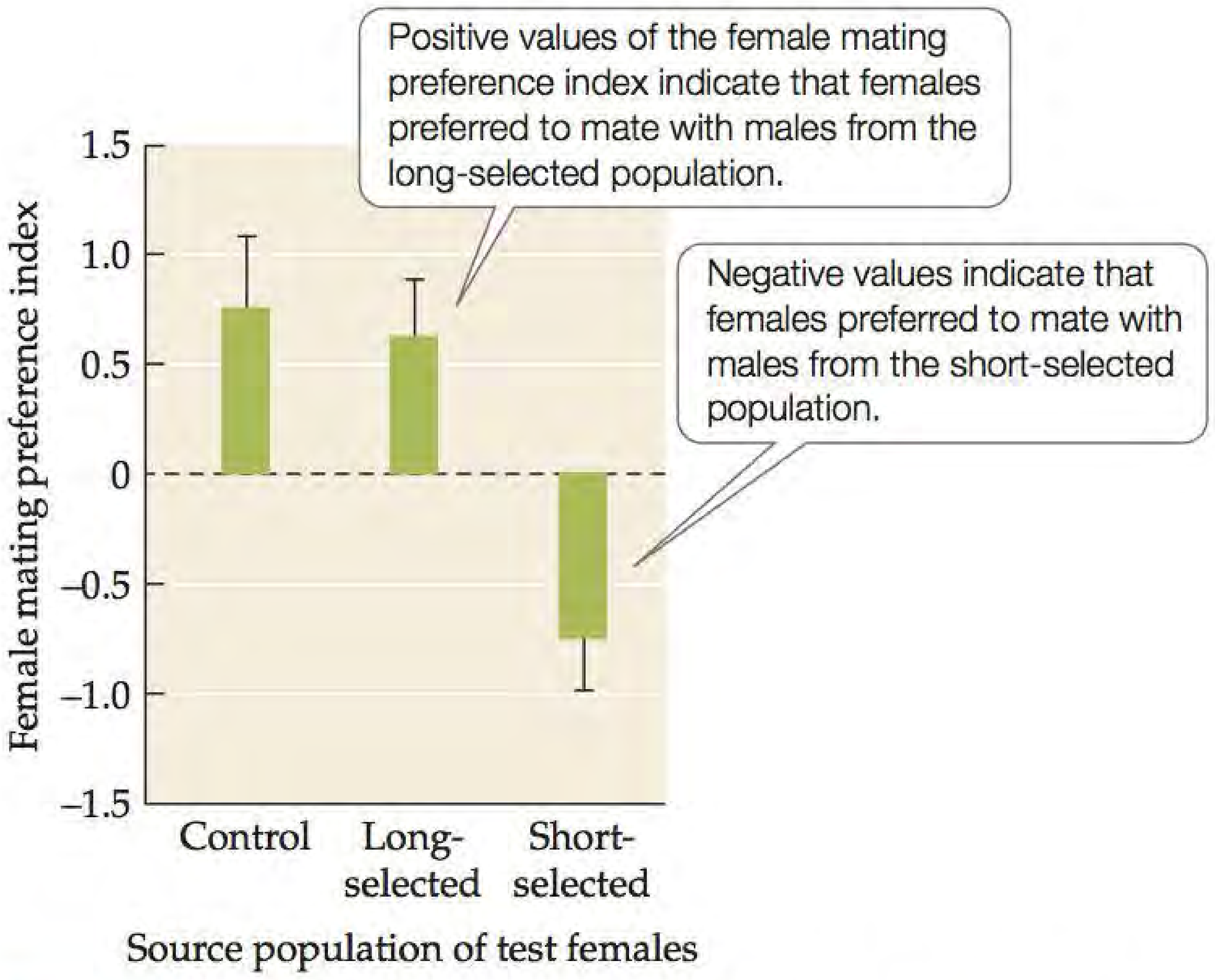


Figure 8.17 Mating Preferences of Female Stalk-Eyed Flies In mate choice experiments, females from control, long-selected, or short-selected populations could choose between a long- or a short-stalked male. The results show that females from control and long-selected populations prefer to mate with long-stalked males, whereas females from short-selected populations prefer short-stalked males. Error bars show one SE of the mean. (After Wilkinson and Reillo 1994.)

The results we've described so far show that (1) females may benefit from selecting males with long eyestalks because their male offspring will be attractive to the next generation of females and (2) eyestalk length in males are encoded by the same genes (or a correlated set of genes) as female mating preference. These findings are consistent with the sexy son hypothesis. However, other studies are consistent with the handicap hypothesis, which posits that good genes are passed to both the sons and daughters of choosy females. For example, David et al. (1998) found that eyestalk length in male stalk-eyed flies was correlated with overall health and vigor. This result suggests that the sons and daughters fathered by males with long eyestalks are likely to be healthier and more vigorous than the offspring of other males.

What is true for stalk-eyed flies is also true for many other species: females receive a variety of direct and indirect benefits when they select their mates. Next, we'll examine a question raised in the opening pages of this chapter: Why are females usually more choosy than males about who they will mate with?

Gamete size, parental care, and ecological factors affect mating behavior

In addition to the differences we have discussed, females and males often differ in how much energy and resources they invest in their offspring. Such investments begin with the production of gametes and may continue in species in which the parents care for their offspring as they develop into young adults. As we'll see, parental investments in offspring, along with ecological factors, can help us to understand the wide range of mating behaviors found in animal populations.

WHY ARE FEMALES USUALLY CHOOSIER THAN MALES?

One clue to explaining female choosiness comes from anisogamy: the difference in size between the egg cells of a female and the sperm cells of a male (see Figure 7.7B). Because female gametes are so much larger than male gametes, a female typically invests more resources in producing a single gamete than does a male, and hence she has more at stake in each one.

Consider a chicken egg. A hen's (unfertilized) egg cell is composed mostly of yolk, and it is as large as the yolk of an egg from the grocery store; in contrast, you would need a microscope to see a rooster's sperm cell. (Some birds invest even more in their eggs than do chickens—see the X-ray photograph of a kiwi carrying an egg in Figure 7.21.) After fertilization, the hen adds other substances to the developing egg, beginning with albumen (the egg white, which is high in protein) and ending with high-calcium secretions (which harden to form the shell). Overall, a hen invests far more in the first stages of reproduction than does a rooster (who contributes sperm and nothing more).

In many species, females continue to invest large amounts of resources as their offspring develop. This is true in chickens: under natural conditions, a hen incubates her eggs to keep them warm, and then cares for her chicks for several weeks after they hatch. The rooster does nothing. What is true for chickens is true for many other species as well: females spend more of their time and energy caring for their offspring than males do.

How do differences in gamete size and parental care relate to mating behavior? As Robert Trivers (1972) pointed out, reproduction is costly, and in species in which females invest more in their offspring than males do, we would expect females to be choosy and males to compete for the right to mate with females. Moreover, since males usually invest relatively little per offspring produced, we would expect that males could produce more offspring during their lifetime than females could. This expectation often holds (**Table 8.1**). When the reproductive potential of males is higher than that of females, selection should favor different mating behaviors in males and females: it should be advantageous for a male to mate with as many females as possible, whereas a female should "protect" her investment by choosing to mate only with males that provide ample resources or that appear to be of high genetic quality.

As we've seen, events in nature are often consistent with these predictions. But what about the exceptions, species in which females compete with one another to mate with males? Assuming that the mating behavior of such species has been shaped by natural selection, in such cases we would expect that males would provide more parental care than females would, leading to competition among females for the right to mate with choosy males.

Field observations generally support this prediction. For example, in the red phalarope (*Phalaropus fulicarius*; see Figure 8.2), once a female lays her eggs, she abandons the nest in search of another mate, leaving the male to incubate the eggs. Or consider the pipefish *Syngnathus typhle*, in which it is the male who becomes pregnant. Males have a special pouch in which they protect, aerate, and nourish the fertilized eggs (Berglund and Rosenqvist 1993). A male does not mate while he is pregnant, but during that time a female can produce additional eggs and mate with several other males. Thus, females have higher reproductive potential than males do, and (as predicted) they compete for the right to mate with males. Males select as their mates the largest, most highly ornamented females; such females produce more eggs than other females do.

TABLE 8.1 Examples of the Reproductive Potential of Males and Females

	MAXIMUM NUMBER OF OFFSPRING PRODUCED DURING LIFETIME	
SPECIES	MALE	FEMALE
Elephant seal	100	8
Red deer	24	14
Human	888	69

Source: Davies et al. 2012.

ECOLOGICAL FACTORS AND MATING BEHAVIOR As we saw in Concept 8.2, the foraging decisions of individuals are affected by ecological factors, such as the presence of predators. Not surprisingly, ecological factors can also affect decisions about mating. Female guppies, for example, mate less often and become less particular in their choice of mates (settling for less brightly colored males) when predators are present (Godin and Briggs 1996). Similar results have been found for many other species. Overall, the evidence shows that in fishes, birds, mammals, and other animals, an individual's decision to mate and its "choosiness" can be altered by such ecological factors as the number and spatial locations of potential mates, the quality of those mates, the availability of food, and the presence of predators or competitors.

Ecological factors can also influence the **mating system**, a term that refers to the number of mating partners that males or females have and the pattern of parental care. A rich variety of mating systems occur in nature (**Table 8.2**), and mating systems can vary not only among closely related species, but even among individuals within a population of a single species. How can we make sense of this variation? In a groundbreaking paper, Emlen and Oring (1977) argued that the diverse mating systems seen in nature result from the behaviors of individuals striving to maximize their reproductive success, or *fitness*.

Let's consider the logic of Emlen and Oring's approach from a male perspective. As mentioned earlier, males typically have greater reproductive potential than females; hence, the reproductive success of males will often be limited by access to potential female mates. Under certain conditions, this imbalance can lead to *polygyny*, a mating system in which one male mates with multiple females in a breeding season. As Emlen and Oring (1977) wrote, "Polygyny occurs if environmental or behavioral conditions bring about the clumping of females, and

TABLE 8.2 Mating Systems

MATING SYSTEM	DESCRIPTION
Monogamy	A male mates with only one female, and she with him. This pairing may last for one or more breeding seasons. In many cases, both parents care for the young.
Polygyny	One male mates with multiple females in a breeding season. The male may control access to these females directly (by fighting with other males) or indirectly (by controlling access to resources that females seek, such as food or good nesting sites). The female usually provides most or all of the parental care.
Polyandry	One female mates with multiple males in a breeding season. The female may defend these males directly (by fighting with other females) or indirectly (by controlling access to food or other resources). The male usually provides most or all of the parental care.
Promiscuity	Both males and females mate with multiple partners in a breeding season.

males have the capacity to monopolize them." For example, the availability of food or nest sites may affect where females are found. Whether females settle close to or far away from one another may determine whether a male can acquire and defend more than one mate (**Figure 8.18**).

Experimental studies in birds, fishes, and mammals have illustrated particular cases in which females clump together in high-resource areas—and the males then follow the females to those same areas. Moreover, in some cases, field observations indicate that the availability of resources is correlated with both the locations of females and the mating system. For example, Martin and Martin (2007) found that the brushtail possum (*Trichosurus cunninghami*) was monogamous in a habitat where food and nest sites (and hence females) were widely separated, but polygynous in a habitat where food and nest sites (and hence females) were located closer to one another. Similarly, Lukas and Clutton-Brock (2013) found that monogamy usually occurs in mammalian species where it is difficult for males to defend access to more than one breeding female—as hypothesized by Emlen and Oring's original paper.

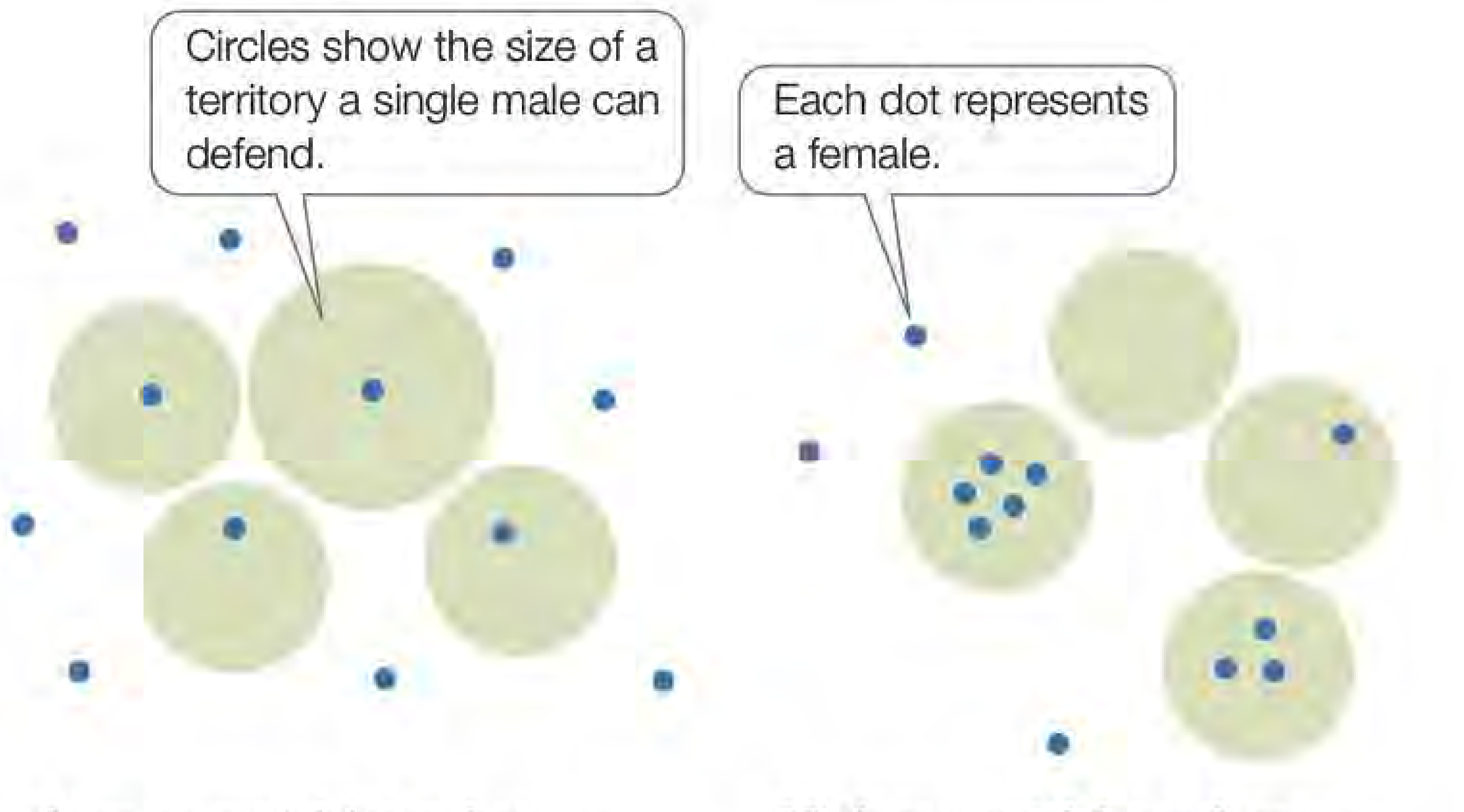


Figure 8.18 Ecological Factors Can Affect the Potential for Polygyny In this diagram, dots represent the locations of females, and circles show the size of a territory that a male can defend.

CONCEPT 8.4
There are advantages and disadvantages to living in groups.

Living in Groups

Individuals of the same species often cluster together, forming groups. Familiar examples of such groups include herds of horses, prides of lions, schools of fish, and flocks of birds. How might the individuals in a group benefit from belonging to the group? And are there disadvantages to communal life that might limit the size of a group or prevent its formation altogether?

Benefits of group living include access to mates, protection from predators, and improved foraging success

Members of a group can enjoy higher reproductive success than solitary individuals. This is clear for males that hold high-quality territories, and it may also be true for females in such territories because they may gain access to good breeding sites or abundant supplies of food. Like the females of a lion pride, group members may also share the responsibilities of feeding and protecting the young, which can benefit the parents (who may have more time to obtain food for themselves) as well as the offspring (who may be both better fed and better protected).

Living in a group can provide other advantages as well, such as a reduced risk of predation. In some cases, the individuals in the group can band together to discourage attack (**Figure 8.19**). Moreover, predators are often detected sooner when they approach a group than when they approach a single individual. As a result, they are less likely to surprise their prey, which causes the predators' attack success rate to drop. For example, goshawks were successful in killing wood pigeons about 80% of the time when they attacked a

Figure 8.19 **A Formidable Defense** A group of musk oxen that circles is a very difficult target for predators.

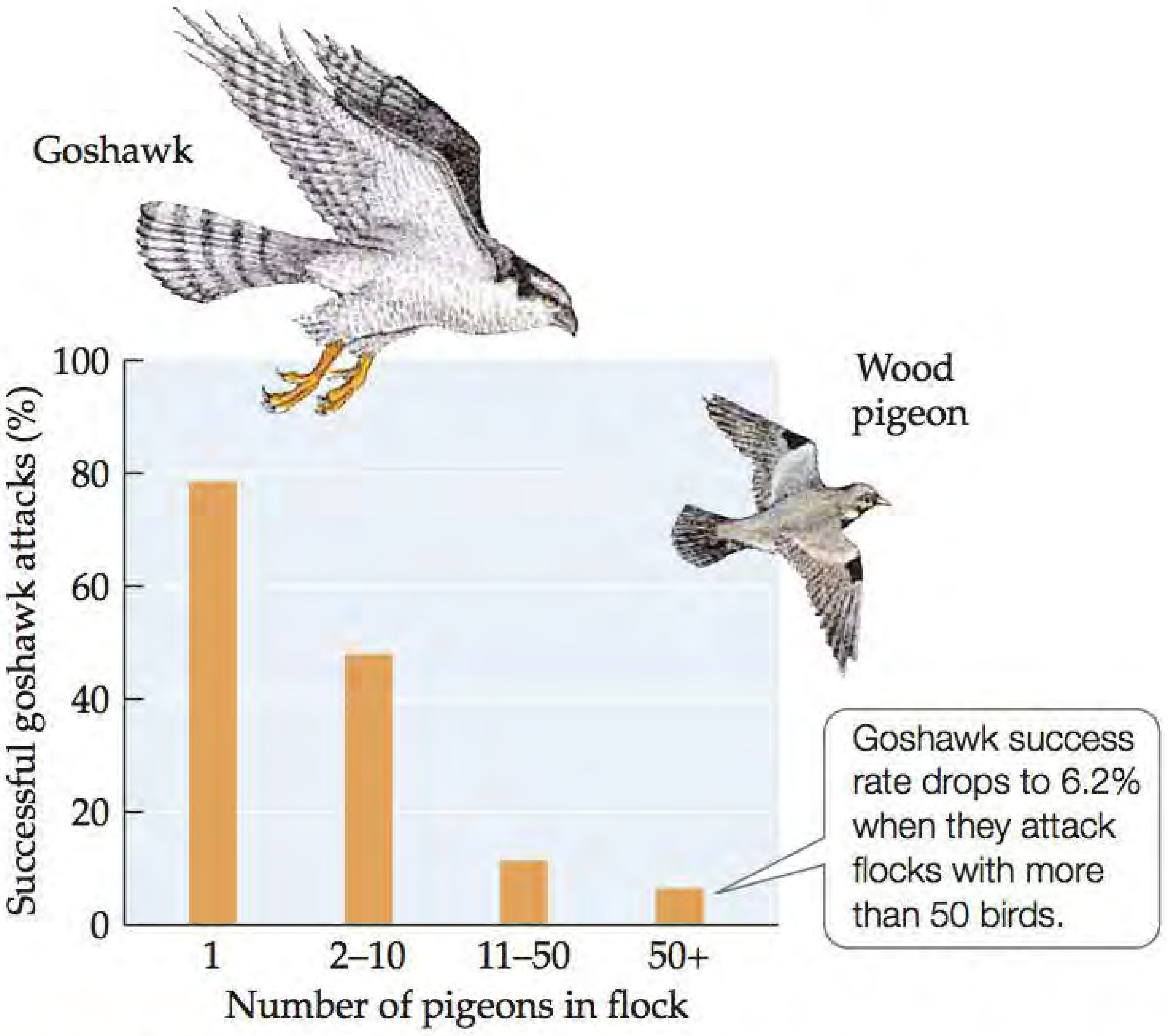


Figure 8.20 **Safety in Numbers** The success rate of a goshawk attacking wood pigeon prey plummets when it attacks a large flock. (After Kenward 1978.)

single pigeon, but when they attacked pigeons in a large flock, they were detected sooner, and their success rate plunged (**Figure 8.20**).

In other cases, group members do not cooperate against predators, yet individuals in a group still have a lower risk of predation than they would on their own. One reason for this is that as the number of individuals in a group increases, the chance of being the one attacked decreases, a phenomenon known as the **dilution effect**. In **Analyzing Data 8.1**, you can see whether the dilution effect applies to a marine insect attacked by fish predators. Furthermore, if group members respond to a predator by scattering in different directions, they may make it difficult for the predator to select a target, thus causing the predator's attack success rate to drop.

Group members may also experience improved foraging success. Two or more lions, for example, can bring down much larger prey than a single lion could tackle on its own. Furthermore, lions, killer whales, wolves, and

ANALYZING DATA 8.1 Does the Dilution Effect Protect Individual Ocean Skaters from Fish Predators?

Individuals in a group may gain protection from predators because of the dilution effect: when a predator attacks, the larger the number of prey individuals in the group, the smaller the chance that any particular member of the group will be the victim.

Foster and Treherne* tested whether the dilution effect occurred when a predatory fish (*Sardinops sagax*) attacked groups of a marine insect, the ocean skater (*Halobates robustus*). A subset of their data is presented in the table, which shows the number of predator attacks (per 5 minutes) on ocean skater groups differing in size.

NO. INSECTS IN GROUP	NO. GROUPS OBSERVED	NO. ATTACKS (PER 5 MINUTES PER GROUP)
1	3	15; 6; 10
4	2	16; 8
6	3	9; 12; 7
15	2	7; 10
50	2	15; 11
70	2	14; 7

1. Calculate the average number of attacks (per 5 minutes) for each group size. Do the fish predators show a clear preference for attacking small groups over large groups (or vice versa)? Explain.
2. For each group size, convert the average that you calculated for question 1 into the average number of attacks *per individual* (per 5 minutes). Is there a consistent relationship between the average number of attacks per individual (per 5 minutes) and group size? Explain.
3. Are these results consistent with the dilution effect?

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*Foster, W. A. and J. E. Treherne. 1981. Evidence for the dilution effect in the selfish herd from fish predation on a marine insect. *Nature* 293: 466–467.

See the companion website for a similar ANALYZING DATA exercise.

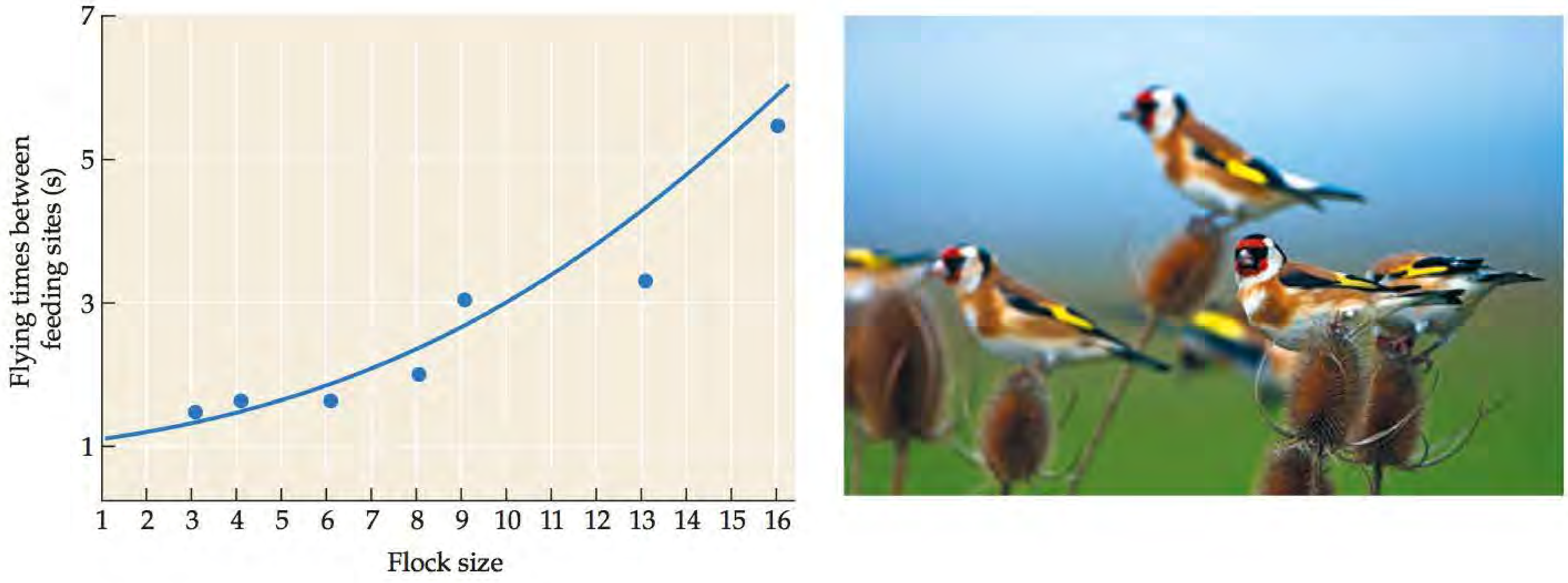


Figure 8.21 Traveling in a Group A study of goldfinches (*Carduelis carduelis*) in groups of seven different sizes showed that the amount of time the birds spent flying between feeding sites increased with the size of the flock. (After Glück 1987.)

? A goldfinch feeding in a flock eats more seeds per hour than does a goldfinch feeding alone. Can that benefit be compared directly with the cost shown in this figure? If not, what other information would you need to make this comparison?

many other predators may coordinate their attacks, such that the actions of one predator drive prey into the waiting jaws of another. Herbivores may also forage more effectively when in groups than when on their own.

Costs of group living include greater energy expenditures, more competition for food, and higher risks of disease

In one study of group living, a goldfinch (*Carduelis carduelis*) in a flock of six birds consumed (on average) 20% more seeds per unit of time than did a bird feeding on its own, because goldfinches in a flock spent more time eating and less time scanning for predators than did goldfinches feeding on their own (Glück 1987). But the increase in the number of seeds eaten per unit of time by a goldfinch in a flock has a downside: as the group size increases, group members deplete the available food more rapidly, which means the birds must spend more of their time flying between feeding sites (**Figure 8.21**). Traveling in search of food takes time and energy, and it can increase the risk of being spotted by predators.

Competition for food can also become more intense as the size of a group increases. As a result, a member of a large group may spend more time and energy fighting for food than would a member of a smaller group (or a solitary individual). In particular, in groups with a dominance hierarchy, subordinate group members can spend much of their time and energy on interacting with group members. For example, in a study on the cichlid fish *Neolamprologus pulcher*, subordinates spent more of their energy on submissive behaviors (appeasing dominant group members) than they did on any other activity.

Finally, members of a large group may live closer together or come into contact with one another more often than do members of a small group. As a result, parasites and diseases often spread more easily in large groups than in small groups; we'll return to this topic in Concept 13.5.

Group size may reflect a balance between the costs and benefits of group living

If we apply the principles discussed in this chapter to group size, we might predict that groups should be of a size at which the benefits of belonging to a group exceed the costs. For example, using an approach similar to that introduced in Concept 8.2, we could predict that groups will have an "optimal" size—the size at which the net benefits received by its members are maximized. However, as shown in **Figure 8.22**, unless group members can prevent other individuals from joining the group once an optimal size is reached, the observed group size may be larger than the optimal size. In addition, it can be very difficult to measure all the benefits and costs of group living; it is particularly challenging to quantify both costs and benefits with a single "currency," such as energy use or offspring production.

In general, an argument like that in Figure 8.22 suggests that it may be advantageous for individuals to belong to groups that are larger than the optimal size, but not so large that a new arrival would do better on its own. Such an intermediate-sized group might be large enough to reduce the risk of predation, but small enough to avoid running out of food. Using an overall measure of individual condition (level of stress as measured by fecal concentrations of the hormone cortisol), Pride (2005) found that ring-tailed lemurs in groups of intermediate sizes were less stressed than lemurs that

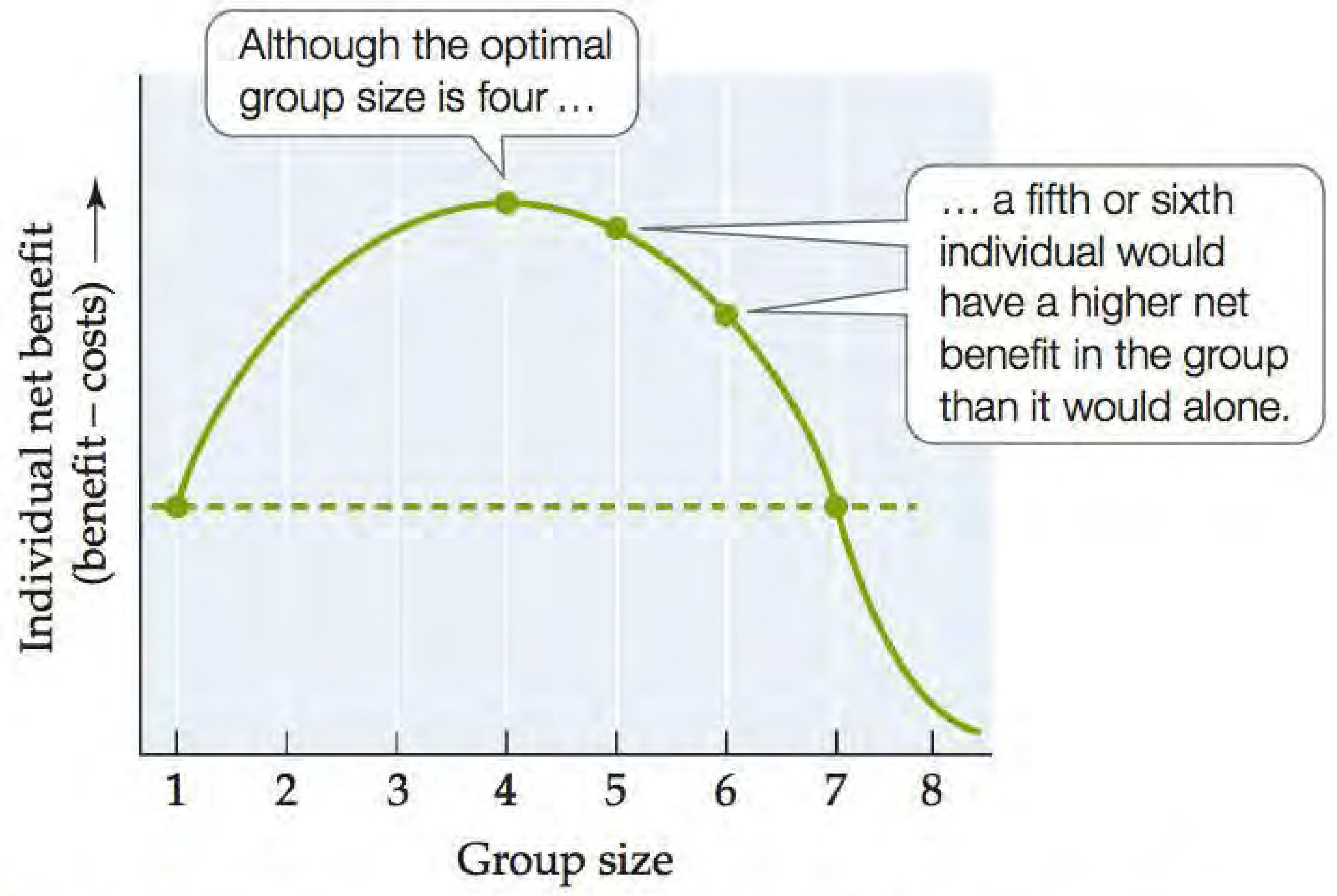


Figure 8.22 Should a New Arrival Join the Group? In this hypothetical example, the net benefit to an individual group member is maximized at the optimal group size of four. However, a new arrival would have a greater net benefit if it joined a group of size four than if it remained alone. Unless existing group members can prevent new arrivals from joining the group, new arrivals should continue to join until the group has reached a size of seven—at that point, the individual would do better on its own than in the group.

belonged to smaller or larger groups. Similarly, Creel and Creel (1995) found that the per capita intake of food for Tanzanian wild dogs chasing prey was greatest for packs of intermediate sizes.

A CASE STUDY REVISITED

Baby Killers

Can an evolutionary perspective on behavior help us to understand infanticide? It turns out that the males of many species kill the young of their potential mates. For example, male langur monkeys (*Semnopithecus entellus*) kill the infants of females in their social group. This behavior appears to increase the reproductive success of the murderous males: DNA paternity analyses showed that infanticidal male langurs were not related to the infants they killed but were related to the females' subsequent offspring (Borries et al. 1999). Infanticide by males has been documented in dozens of other species, including horses, chimpanzees, bears, and marmots. Infanticide by males appears to be adaptive in many cases: it reduces the time that females spend between pregnancies, thus enabling the males to sire more offspring than they otherwise could.

But in some species, females commit infanticide. For example, female giant water bugs (*Lethocerus deyrollei*) and female wattled jacanas (*Jacana jacana*) slaughter the eggs or young of their own species. While gruesome, this behavior also makes evolutionary sense: in these species, the males provide most or all of the parental care, and the females have higher reproductive potential than the males. Thus, as is true for male lions and langurs, the infanticidal behavior of female water bugs and jacanas appears to be adaptive: by killing the young, a female bug or bird shortens the time before the male is willing to mate again, thus potentially increasing her own reproductive success.

What about other puzzling behaviors mentioned in this chapter's Case Study? Recall that female fruit flies (*Drosophila melanogaster*) sometimes lay their eggs in foods that are high in ethyl alcohol. But this behavior is not as strange as it first appears: evidence suggests that it provides a behavioral defense against the wasp *Leptopilina heterotoma*. Females of this wasp lay their eggs on fruit fly larvae; when an egg hatches, the young wasp burrows through the body of the fly larva, consuming and killing it. A fruit fly larva infected by this wasp will preferentially choose to eat foods that are high in alcohol content, such as rotting fruit. Consuming foods containing high concentrations of alcohol harms the fruit fly larvae, but the benefits of this action outweigh its costs: exposure to alcohol often kills the wasps, thereby increasing the overall chances that the larvae will survive. In addition, Kacsoh et al. (2013) showed that adult female fruit flies altered their egg-laying behavior in response to the presence of wasps. In the absence of wasps, the fruit flies laid about 40% of their eggs in high-alcohol foods, but when female wasps were present, the fruit flies laid over 90% of their eggs in high-alcohol foods. This behavior increased the survival of fruit fly larvae exposed to wasps (**Figure 8.23**), suggesting that the behavior can be viewed as a type of preventative medicine.

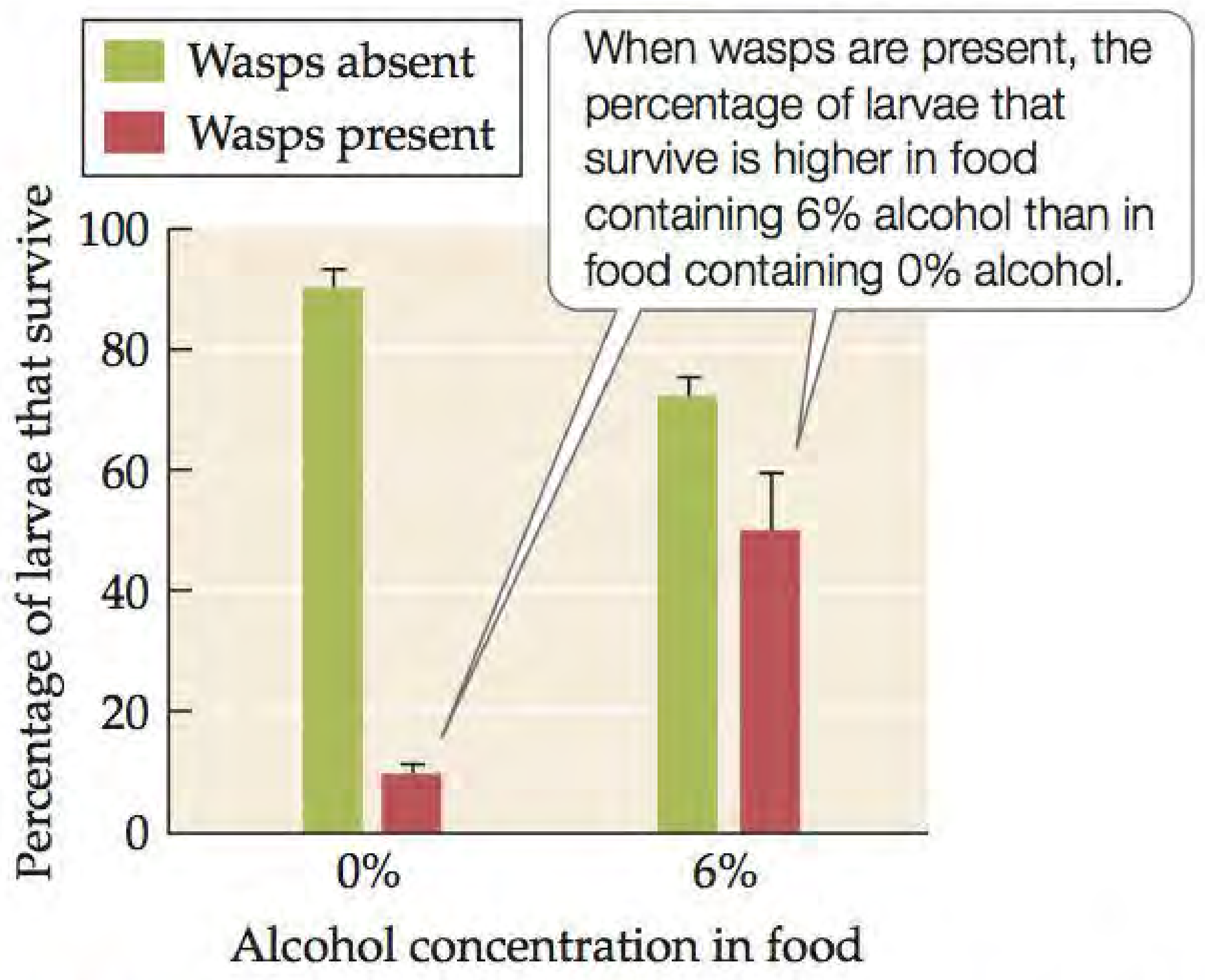


Figure 8.23 Fruit Flies Medicate Their Offspring Female fruit flies (*Drosophila melanogaster*) laid most of their eggs in foods containing alcohol when females of the wasp *Leptopilina heterotoma* were present. This behavior increased the percentage of fruit fly larvae that survived to adulthood. Error bars show one SE of the mean. (After Kacsoh et al. 2013.)

? In the absence of wasps, what is the cost (in terms of reduced larval survival) of laying eggs on food containing 6% alcohol? When wasps are present, what is the benefit?

CONNECTIONS IN NATURE
Behavioral Responses to Predators Have Broad Ecological Effects

As you've seen, individuals often change their behavior in response to predators. For example, in Concept 8.2, we saw that when exposed to recordings of sounds made by predators, song sparrows fed their young less often, built their nests in less desirable areas, and spent less time incubating their eggs (Zanette et al. 2011). What were the consequences of these behavioral changes?

Zanette and colleagues found that when song sparrow parents altered their behavior in response to a perceived high risk of predation, their offspring lost body heat more rapidly (**Figure 8.24A**) and weighed less than did the offspring of sparrows exposed to recordings of nonpredators. These effects on individual offspring appear to have caused the number of offspring produced per year to decline (**Figure 8.24B**). Overall, the results of this study suggest that fear of predation alters the behavior of song sparrows in ways that decrease their reproductive success and may cause their population sizes to drop.

Behavioral responses to predators can also affect ecosystem processes, such as the decomposition of leaves and other plant litter in soil. As Hawlena and colleagues (2012) described, this effect occurs indirectly: the presence of spider predators initiated a series of events in their grasshopper prey that ultimately slowed the decomposition of plant litter. How did this happen? When the researchers raised grasshoppers in the presence of predators, the grasshoppers became physiologically stressed, one consequence of which was that they required more energy to maintain their basic body functions. This demand for additional energy appears to have altered their foraging behavior, leading the grasshoppers to increase their consumption of foods that are high in carbohydrates (and thus in energy) but low in nitrogen. Thus, grasshoppers stressed by predators had a higher carbon:nitrogen ratio in their bodies than did grasshoppers raised in the absence of predators. Although this change in nutrient content did not affect the decomposition of the grasshoppers' own bodies, it did decrease the decay of plant materials in the soil. This probably happened because the altered carbon:nitrogen ratio in the decomposing bodies of grasshoppers affected the carbon:nitrogen ratio in the soil, which in turn affected the community of soil microorganisms that decompose leaves and other plant matter.

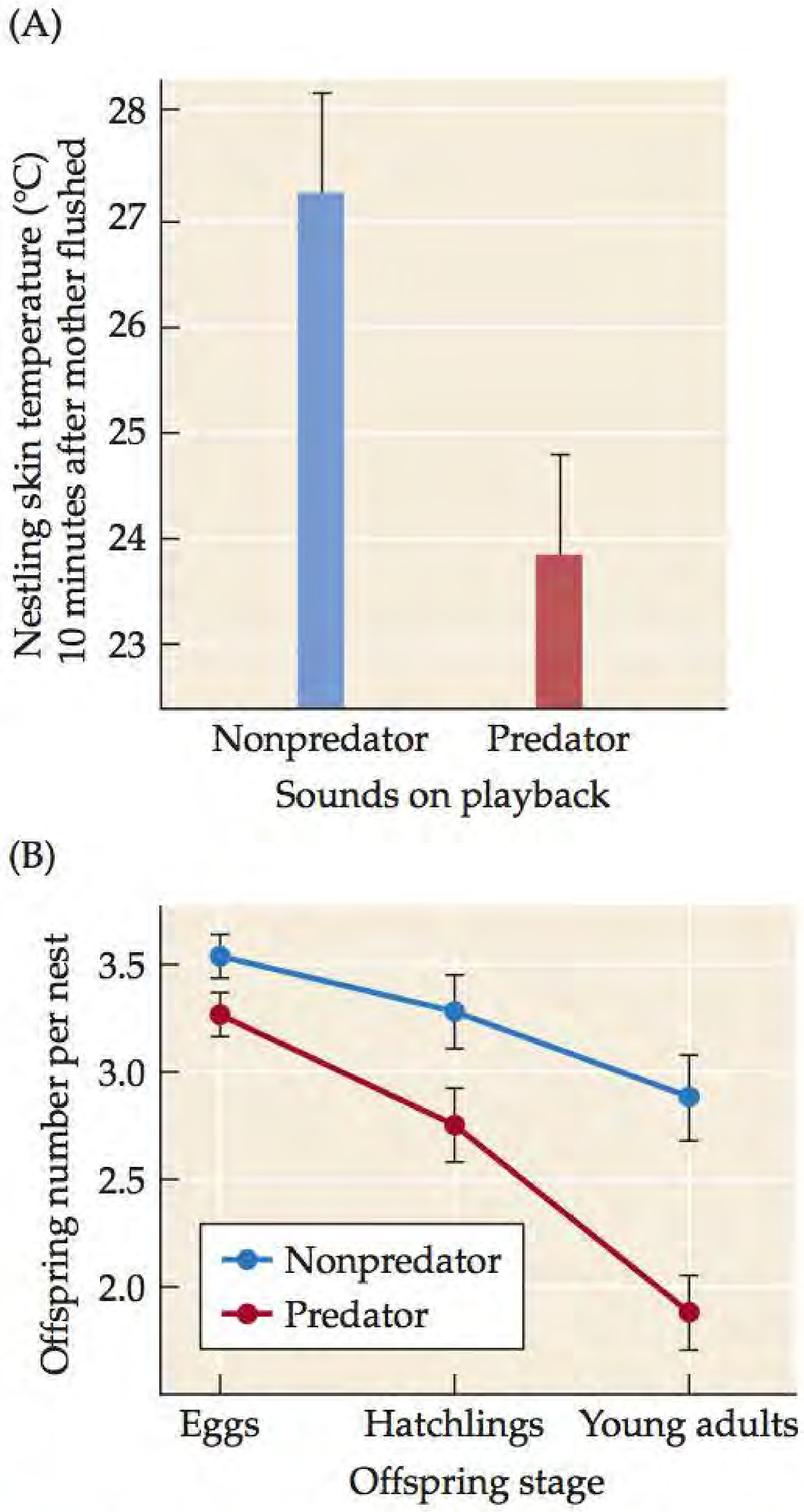


Figure 8.24 Costs of Fear (A) The rate at which young song sparrows lost body heat was higher for offspring of birds exposed to playbacks of predators than it was for offspring of parents exposed to playbacks of nonpredators. Error bars show one SE of the mean. (B) Fewer offspring were produced in nests exposed to playbacks of predators than in nests exposed to playbacks of nonpredators. Error bars show ± one SE of the mean. (After Zanette et al. 2011.)

? Estimate the cost of fear on the number of offspring that survived to young adulthood.

Summary

CONCEPT 8.1 An evolutionary approach to the study of behavior leads to testable predictions.

- Animal behaviors can be explained in terms of their immediate, or proximate, causes or in terms of their evolutionary, or ultimate, causes. Most research in behavioral ecology addresses ultimate causes.
- An individual's ability to survive and reproduce depends in part on its behavior. This observation suggests that natural selection will favor individuals whose behaviors make them efficient at activities such as foraging, obtaining mates, and avoiding predators.
- Animal behaviors are influenced by genes as well as by environmental conditions.
- By assuming that genes affect behaviors and that natural selection has shaped behaviors over time, we can predict how animals will behave in particular situations.

CONCEPT 8.2 Animals make behavioral choices that enhance their energy gain and reduce their risk of becoming prey.

- Optimal foraging theory predicts that foraging animals will maximize their net energy gain per unit of feeding time and per unit of energy invested in seeking, capturing, and extracting food resources.
- Individuals often alter their foraging decisions when predators are present. A perceived risk of predation can also alter foraging patterns, even in the absence of actual predation.
- Prey exhibit a wide range of behaviors that can help them avoid being seen by predators, detect predators, prevent attack, or escape once attacked.

CONCEPT 8.3 Mating behaviors reflect the costs and benefits of parental investment and mate defense.

- Within a species, males are often larger or more brightly colored than females, or they may possess unusual weapons or have gaudy ornaments. Such differences between males and females of the same species can result from sexual selection.
- A female may receive indirect genetic benefits when she chooses to mate with a male that has certain features, such as a costly and unwieldy ornament. According to the handicap hypothesis, if she chooses a male that can support such an ornament, it is likely that he will pass on good genes to both her sons and her daughters. According to the sexy son hypothesis, the female receives indirect genetic benefits through her sons, who will themselves be attractive and produce many grandchildren.
- In most species, females invest more in their gametes and provide more parental care than males do. In this situation, males and females have different interests: it is to a male's advantage to mate with as many females as possible, whereas a female should "protect" her investment by mating with those males that provide the most resources or that appear to be of high genetic quality.
- In the rare cases in which males typically provide more parental care than females do, it is the male who is the choosy partner.
- The rich variety of mating systems seen in nature result from the behaviors of individuals striving to maximize their reproductive success.

CONCEPT 8.4 There are advantages and disadvantages to living in groups.

- Benefits of group living include access to mates, protection from predators, and improved foraging success.
- Costs of group living include greater expenditures of energy, increased competition for food, and higher risks of disease.
- Group size may reflect a balance between the costs and benefits of group living; in some cases, this balance appears to have caused groups to be larger than the optimal size.

Review Questions

1. Distinguish between proximate and ultimate explanations of animal behavior.
2. Explain the links between the following: natural selection, heritable behaviors, adaptive evolution, and ultimate explanations of animal behaviors.
3. Describe how the presence of a predator may alter an individual's foraging decisions. Can fear of predators have similar effects, even in the absence of actual predators? Explain.
4. What is sexual selection? Summarize the evidence supporting the claim that differences between males and females can result from sexual selection.
5. Describe an example in which group living leads to both benefits and costs.
6. Consider two bird species that forage for insects that live in shrubs. The shrubs have a clumped, patchy distribution throughout their habitat. The two bird species have the same ability to locate, capture, and consume the insects. However, one species (species A) uses less energy to fly from patch to patch than the other species (species B). According to the marginal value theorem, which bird species should spend more time in each patch, and why?

Hone Your Problem-Solving Skills

Humans have added billions of tons of plastic waste to the world's oceans. Physical forces and UV light break down this waste into ever smaller "microplastics" (plastic particles less than 5 mm in size) that are eaten by fish larvae and other marine animals. Can the consumption of microplastics impair behaviors that affect survival and reproduction? To find out, researchers exposed larvae of the Eurasian perch (*Perca fluviatilis*) to concentrations of microplastics observed in nature (average and high levels). In three separate experiments, they tested whether microplastics affected (1) distance (mm) perch larvae moved during a 3-minute observation period, (2) responsiveness of perch larvae to an alarm cue, and (3) percentage of perch larvae still alive after 24 hours of continuous exposure to a predator, juvenile pike (*Esox lucius*). Perch larvae typically "freeze," or remain motionless, when a chemical alarm cue is released by other perch larvae; in the second experiment, alarm cue responsiveness was measured as the proportional increase in the amount of time perch larvae spent performing the freezing behavior when exposed to the alarm cue (Lönnstedt and Eklöv 2016). Results are shown in the table.

1. Summarize the results for experiment 1, on distance moved. If microplastics have similar effects in nature, what consequences may that have for perch larvae in the wild?
2. Experiment 2, on freezing behavior, had two sets of controls. Describe these controls and explain why each was used.
3. Summarize the results for the experiment on freezing behavior. Are these results consistent with the results from experiment 3, on survival after exposure to a predator? Explain.

MICROPLASTIC CONCENTRATION (PARTICLES/M^3)	DISTANCE MOVED (MM)	INCREASE IN FREEZING BEHAVIOR		PERCENTAGE SURVIVING AFTER 24 HOURS WITH PREDATOR
		ALARM CUE ADDED	SEAWATER ADDED	
Control (0)	176.3	3.5	0	47
Average (10,000)	161.2	1.4	0	33
High (80,000)	139.4	0	0	0

ON THE COMPANION WEBSITE

ecology4e.sinauer.com

The website includes companions to all of the Analyzing Data exercises, Online Quizzes, Flashcards, Suggested Readings, and more. In addition, the following resources are available for this chapter:

Hands-On Problem Solving

8.1 Eating on a Budget: Balancing Costs and Benefits of Foraging

Web Extensions

8.1 The Sound of Worms

8.2 Fear of Predation Experiment

Unit 3

Populations

9 Population Distribution and Abundance

KEY CONCEPTS

CONCEPT 9.1 Populations are dynamic entities that vary in size over time and space.

CONCEPT 9.2 The distributions and abundances of organisms are limited by habitat suitability, historical factors, and dispersal.

CONCEPT 9.3 Many species have a patchy distribution of populations across their geographic range.

CONCEPT 9.4 The dispersion of individuals within a population depends on the location of essential resources, competition, dispersal, and behavioral interactions.

CONCEPT 9.5 Population abundances and distributions can be estimated with area-based counts, distance methods, mark–recapture studies, and niche models.

From Kelp Forest to Urchin Barren: A Case Study

Stretching over 1,600 km of the Pacific Ocean to the west of Alaska, the mountainous Aleutian Islands are often shrouded in fog and battered by violent storms. The islands have few large trees, and except for the eastern islands that once were connected to the mainland, they lack the terrestrial mammals that are found on the mainland, such as brown bears, caribou, and lemmings. There is abundant marine wildlife in the surrounding waters, however, including seabirds, sea otters, whales, and a variety of fishes and invertebrates.

Although there are few trees on land, the nearshore waters of some Aleutian islands harbor fascinating marine communities known as kelp forests, made up of brown algae such as *Laminaria* and *Nereocystis*. Dense clusters of kelp rise from their holdfasts on the sea bottom toward the surface, producing what feels like an underwater forest (**Figure 9.1**). Other, nearby islands do not have kelp forests. Instead, the bottoms of their nearshore waters are carpeted with sea urchins and support few kelp or other large algae. Areas with large numbers of urchins are called urchin barrens, since they contain far fewer species than kelp forests do. Why are some islands surrounded by kelp forests and others by urchin barrens?

One possibility is that islands with kelp forests differ from islands without kelp forests in terms of climate, ocean currents, tidal patterns, or physical features such as underwater rock surfaces. But no such differences have been found, leaving us to look for other reasons why some islands have kelp forests while others do not. Because urchins feed on algae and can eat vast quantities of it, investigators suspected that grazing by urchins might prevent the formation of kelp forests.

This hypothesis was tested in two ways. First, studies in the Aleutian Islands and elsewhere along the Alaskan coast consistently showed that kelp forests were not found in regions where there were many large urchins. Although such correlations did not prove that urchins suppress kelp forests, the fact that a number of studies found the same result suggested that urchins might determine where kelp forests are located. Second, the effect of urchins was tested in an experiment that

Figure 9.1 Key Players in the Forests of the Deep The bull kelp *Nereocystis luetkeana* is one of several species that make up the kelp forests found off the coasts of some Aleutian islands. Research shows that the presence or absence of kelp forests near these islands is influenced by both sea urchins and sea otters.

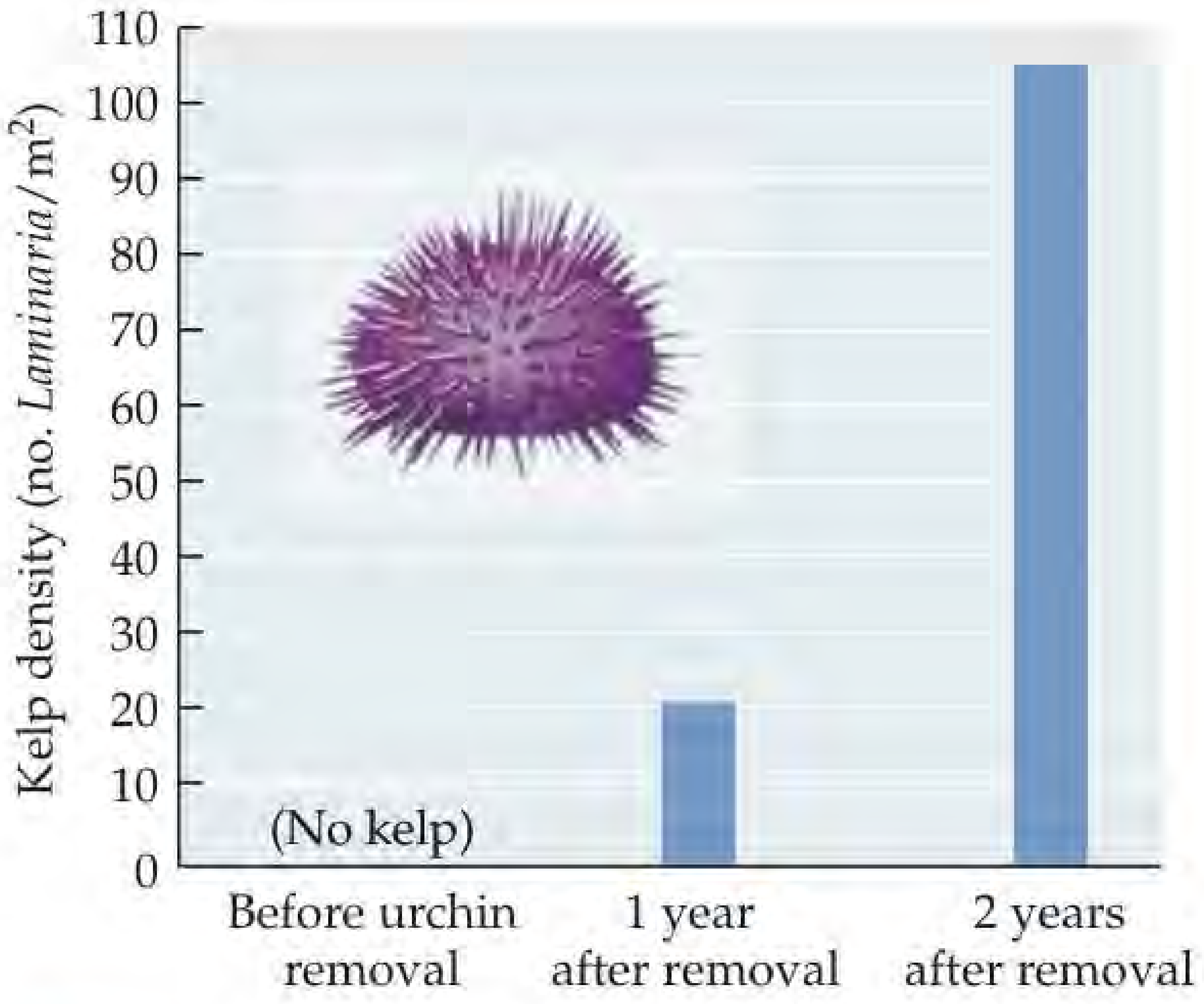


Figure 9.2 Do Sea Urchins Limit the Distribution of Kelp Forests? Mean densities of the kelp *Laminaria* in 50 m^2 plots increased dramatically after urchins were removed. (After Duggins 1980.)

measured change in kelp densities in several 50 m^2 plots containing urchins and in similar, nearby 50 m^2 plots from which urchins were removed (Duggins 1980). There were no kelp in any of the plots at the start of the experiment, and kelp densities remained at zero in the plots where urchins remained. In the plots from which urchins had been removed, however, the density of *Laminaria* rose to 21 individuals per square meter in the first year and reached 105 individuals in the second year (**Figure 9.2**). *Laminaria* is a dominant member of kelp forest communities, so these results suggested that kelp forests would grow in the absence of urchins.

These and other results indicated that the presence or absence of urchins is an answer to the question of why some Aleutian islands have kelp forests and others do not. But this answer just shifts the question from what determines the locations of kelp forests to what determines the locations of urchins. As we'll see, a more complete answer to our question about why kelp forests are found in some areas but not others turns out to depend on the voracious feeding habits of sea otters, which themselves may have become a meal of last resort for killer whales.

Introduction

In this chapter's Case Study, we discussed why kelp forests are found in some places and urchin barrens in others. That discussion focused on a fundamental ecological question: What determines a species' **distribution**, the geographic area where individuals of the species are present? In this chapter and throughout Unit 3, we will also be concerned with the related issue of what determines **abundance**, the number of individuals of a species that are found in a given area. These two issues are related, since the distribution of a species can be viewed as a map of all areas where the abundance of the species is greater than zero.

Ecologists often seek to understand the factors that determine the distributions and abundances of organisms. This task can be challenging because populations are *dynamic*; that is, their distributions and abundances can change greatly over time and space. Such changes affect many aspects of biological communities, including the outcome of species interactions as well as ecosystem processes. Our ability to predict these changes thus serves as a "measuring stick" for how well we understand events in nature.

Knowledge of the factors that influence distributions and abundances also has practical importance for the management of populations of species we harvest (such as fishes or trees) or seek to conserve (such as endangered species). We can best manage or protect such populations if we have a clear understanding of what determines their distributions and abundances. We'll begin our exploration of the factors that influence distribution and abundance by describing populations in more detail.

CONCEPT 9.1

Populations are dynamic entities that vary in size over time and space.

Populations

A **population** is a group of individuals of the same species that live within a particular area and interact with one another. To explore this definition further, what exactly do we mean by "interact"? In species that reproduce sexually, a population might be defined as the group of individuals that interact by interbreeding. In species that reproduce asexually, however, such as dandelions or the fish *Poecilia formosa*, a population must be defined by other kinds of interactions, such as competition for common sources of food. Our definition of a population also incorporates the area over which members of a species interact. If that area is known, as in a population of lizards that live on and move throughout a small island, we can report population abundance either as **population size** (the number of individuals in the population) or as **population density** (the number of individuals per unit of area). For example, if there were 2,500 lizards on an island of 20 hectares (ha), or roughly 50 acres, the population size would be 2,500 lizards, and the population density would be 125 lizards per hectare.

In some cases, the total area occupied by a population is not known. For example, when little is known about how far a sexually reproducing species or its gametes (e.g., plant pollen) can travel, it is difficult to estimate the area over which individuals interbreed frequently and hence represent a single population. For asexual species, similar problems are encountered when we try to estimate the area over which interactions other than interbreeding occur. When the area occupied by a population is not fully known, ecologists use the best available information about the biology of the species to delimit an area within which the size and density of the population can be estimated.

Abundances change over time and space

The number of individuals in a population changes over time. This is true whether abundance is measured on a small spatial scale, such as the number of plants found in a restricted area along a riverbank, or on a much larger spatial scale, such as the number of cod found in the North Atlantic Ocean. At any given time, abundance also differs from one place to another. Some populations differ little in abundance over time and space; others differ considerably.

For example, Richard Root and Naomi Cappuccino (1992) studied abundances of 23 species of herbivorous insects that fed on tall goldenrod (*Solidago altissima*). They studied these insects for at least 6 consecutive years at each of 22 sites in the Finger Lakes region of New York (**Figure 9.3**). These sites were no more than 75 km (47 miles) apart; hence, in any given year, all the sites experienced roughly the same climate conditions. Nevertheless, insect abundances varied from one site to another and from one year to the next. For some species, such

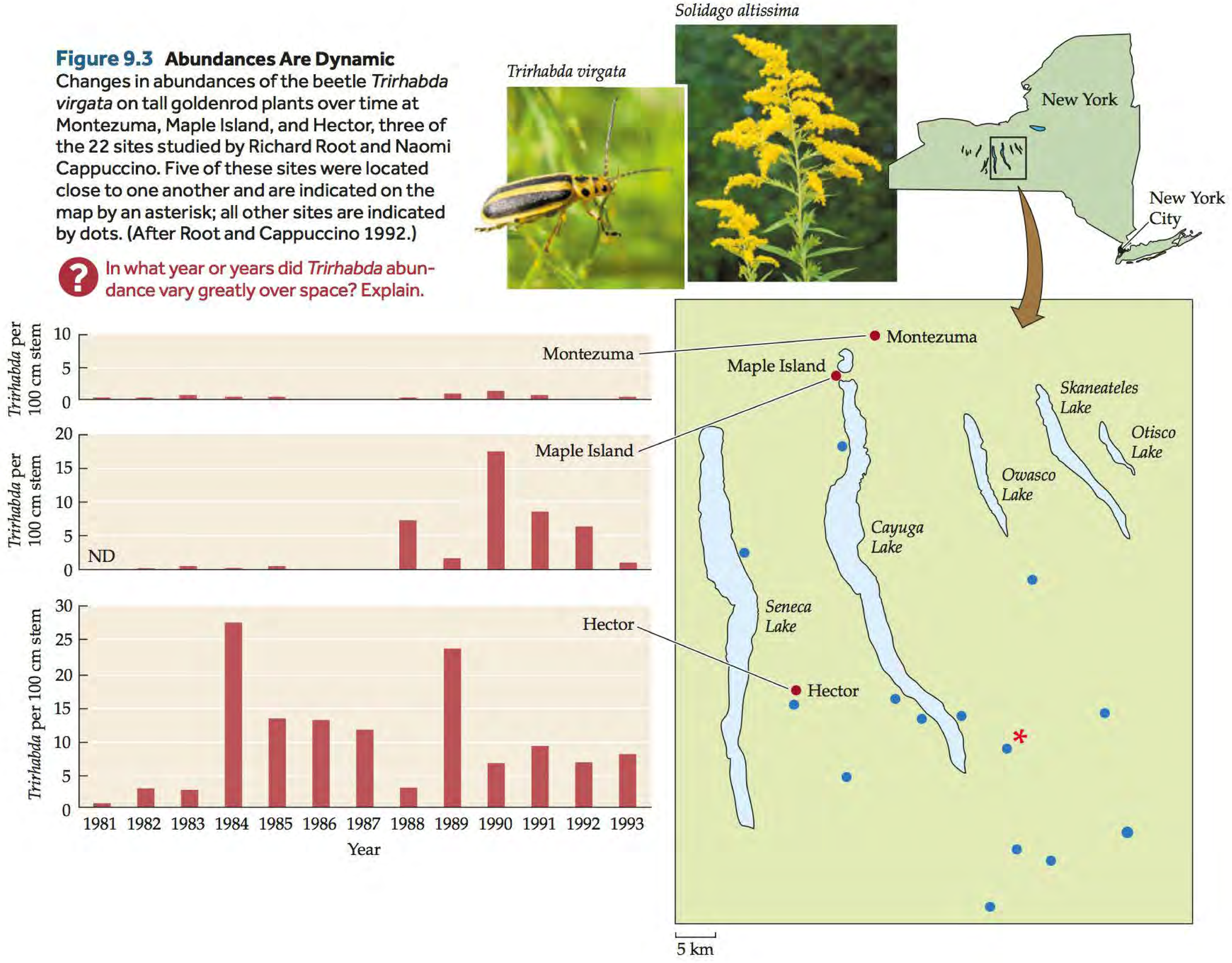


Figure 9.3 Abundances Are Dynamic Changes in abundances of the beetle *Trirhabda virgata* on tall goldenrod plants over time at Montezuma, Maple Island, and Hector, three of the 22 sites studied by Richard Root and Naomi Cappuccino. Five of these sites were located close to one another and are indicated on the map by an asterisk; all other sites are indicated by dots. (After Root and Cappuccino 1992.)

? In what year or years did *Trirhabda* abundance vary greatly over space? Explain.

as the ball gall fly (*Eurosta solidaginis*), abundances varied relatively little. The maximum abundance reached by *Eurosta* over a 6-year period varied sixfold across the 22 sites, from 0.05 insects per stem at the site with the fewest individuals to 0.3 insects per stem at the site with the most individuals. Maximum abundances of other species, however, such as the beetle *Trirhabda virgata*, varied much more (by a factor of 336), ranging from 0.03 to 10.1 insects per stem. Overall, *T. virgata* populations varied considerably in abundance, both from one site to another and over time (see Figure 9.3). We'll return to this topic in Chapters 10 and 11, where we'll examine factors that cause populations to fluctuate in abundance.

Populations are dynamic in another sense as well: individuals move from one population to another, sometimes traveling great distances.

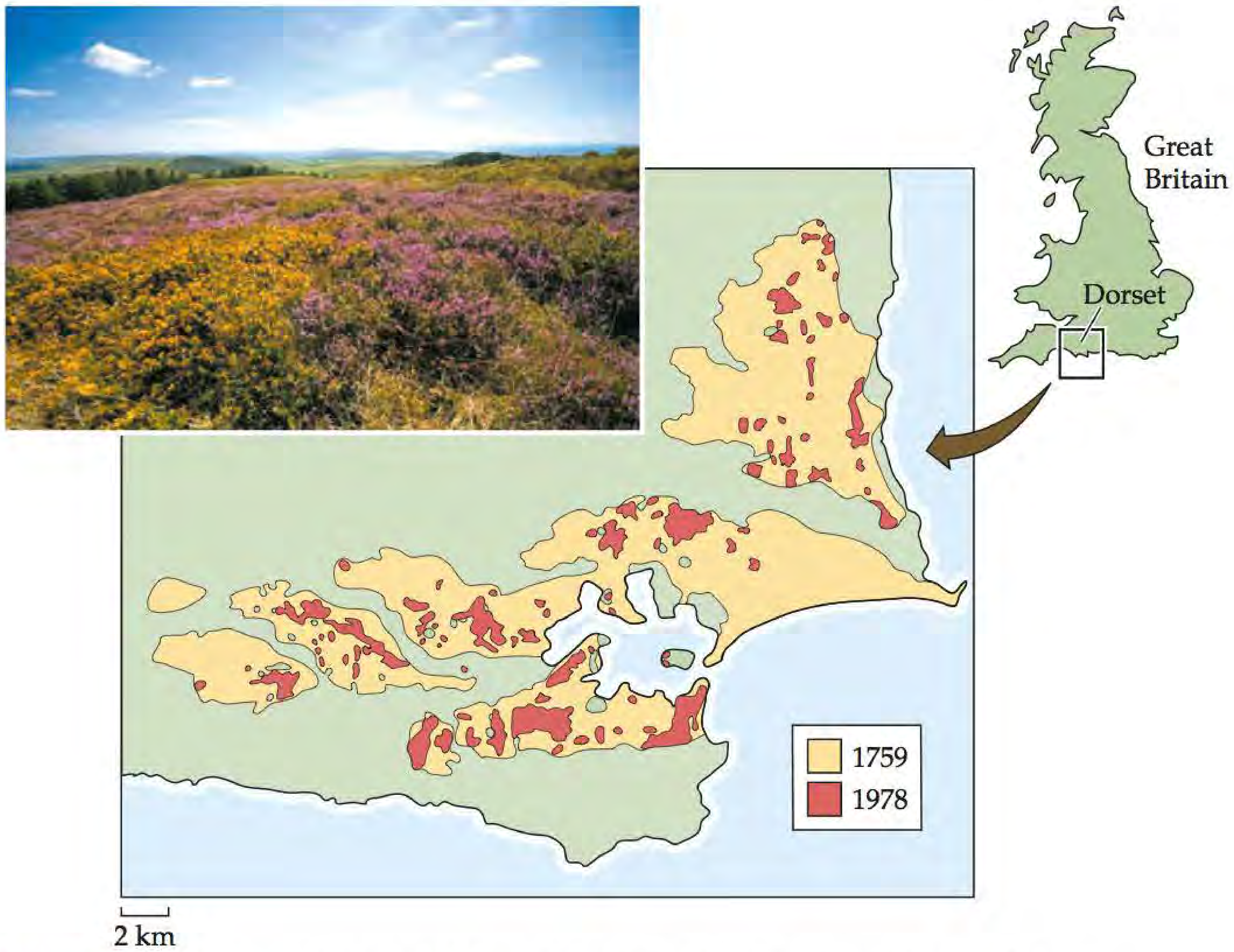


Figure 9.4 Fragmentation of Dorset Heathlands The heathlands of Dorset, England, reached their maximum extent in Roman times, 2,000 years before the present. From 1759 to 1978, the decline of this habitat type accelerated: the total area of heathlands shrank from 400 km^2 to less than 60 km^2, and the number of patches increased greatly. (After Webb and Haskins 1980.)

? How many patches of heathland were present in 1759? In 1978? Use your answers to estimate the average patch size in 1759 and 1978.

Dispersal links populations

Organisms differ greatly in their capacity for movement. In plants, for example, dispersal occurs when seeds move away from the parent plant. Although events such as storms can transport seeds long distances (hundreds of meters to many kilometers; see Cain et al. 2000), dispersal distances in plants are usually small (one to a few tens of meters). In some cases, typical seed dispersal distances are so small that they hardly count as movement. For example, seeds of the forest plant *Viola odorata* have been seen to disperse only 0.002–0.02 m (0.008–0.8 inches) when ants are not present; when ants are present, they may carry these seeds for a few meters. When typical dispersal distances are small, populations of interacting individuals are often found in small areas. At the other end of the spectrum, some whale species travel tens of thousands of kilometers in a single year. Overall, the spatial extent of populations varies tremendously—from very small, in organisms that disperse little, to very large, in species that travel great distances.

Finally, bear in mind that a population may exist in a series of habitat patches or fragments that are spatially isolated from one another but are linked by dispersal. Such a "patchy" population structure can result from features of the abiotic environment, as we'll see later in this chapter. It can also result from human actions that subdivide what were once continuous populations. For example, heaths in England once covered large, continuous areas, but over the past 200 years the development of farms and urban areas has greatly reduced the extent of these plants (**Figure 9.4**). In some cases, this fragmentation results in patches that are so isolated that little dispersal can occur among them, thus breaking a single large population into a series of much smaller populations. In Concept 11.4, we will explore the occurrence and consequences of patchy population structures (*metapopulations*) in more detail.

What are individuals?

As we've seen, a population may cover a single area whose extent depends on the capacity of the species for dispersal, or it may cover a series of spatially isolated patches linked by dispersal. For the many species whose dispersal capabilities are poorly understood, it can be challenging to determine the spatial extent of a population. In addition, for many organisms, it can even be hard to determine what constitutes an individual.

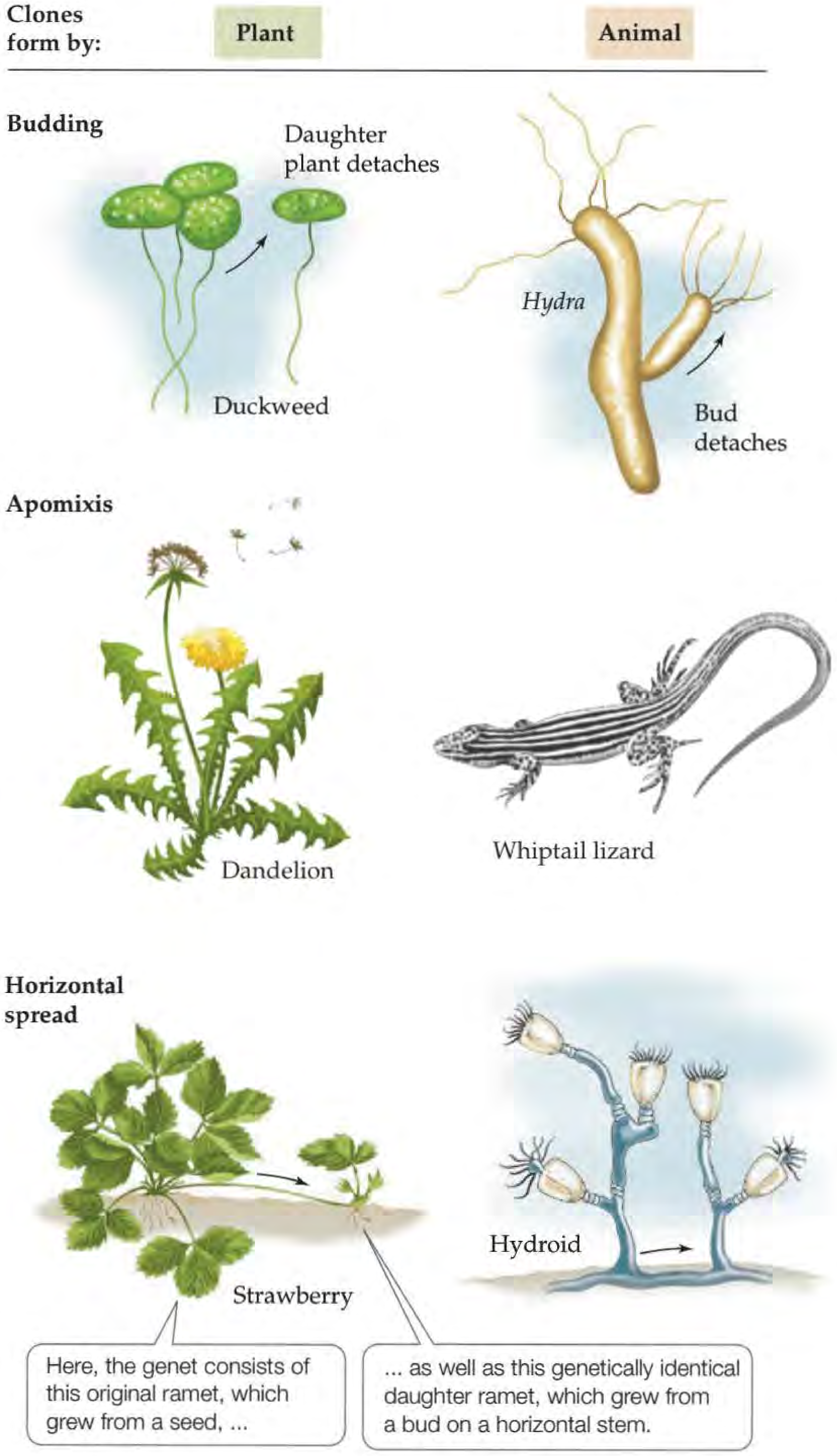
How can there be confusion over what an individual is? Consider the quaking aspen trees (*Populus tremuloides*) in **Figure 9.5**. Like many plant species, an individual aspen can produce genetically identical copies of itself, or **clones**. Aspens produce clones by forming new plants from root buds, while species such as clover and strawberries do so

Figure 9.5 Aspen Groves: One Tree or Many? These quaking aspen (*Populus tremuloides*) growing in western Colorado could represent over 20 different genetic individuals, each established from a seed. However, it is also possible that each of these aspens is actually part of one "tree," having been produced asexually from the root buds of a single genetic individual.

by forming new plants from buds located on horizontal stems, or "runners" (**Figure 9.6**). Among animals, many corals, sea anemones, and hydroids can form clones of genetically identical individuals, as can some frogs, fishes, lizards, and many insects. Some plant clones can grow to enormous sizes (e.g., covering 81 ha, or 200 acres, in aspen clones) or live for extremely long periods (e.g., 43,000 years in *Lomatia tasmanica*, a rare shrub found in Tasmania, Australia).

To cope with the complications that result from the formation of clones, biologists who study such organisms define individuals in several different ways. For example, an individual can be defined as the product of a single fertilization event. Under this definition, a grove of genetically identical aspen trees is a single genetic individual, or **genet**. However, members of a genet are often physiologically independent of one another, and they may in fact compete for resources. Such actually or potentially independent members of a genet are called **ramets**. In strawberries, for example, a rooted plant is considered a ramet because it can persist even if it is not connected to the rest of its genet (see Figure 9.6). Whether we view a patch of strawberries or a grove of aspen trees as one individual or many depends on what we are interested in. If we are interested in evolutionary change over time, the genet level may be most appropriate. In contrast, if we are interested in how independent physiological units compete, the ramet level may be most appropriate.

Now that we've defined populations and considered some of the issues that complicate their study, let's turn to the factors that influence where populations are found and how many individuals they contain.



Here, the genet consists of this original ramet, which grew from a seed, ...

... as well as this genetically identical daughter ramet, which grew from a bud on a horizontal stem.

Figure 9.6 Plants and Animals That Form Clones Many plants and animals reproduce asexually, thereby forming clones of genetically identical individuals. Examples of asexual reproduction include *budding* (in which clonal offspring detach from the parent), *apomixis* (in which clonal offspring are produced from unfertilized eggs; also known as *parthenogenesis*), and *horizontal spread* (in which clonal offspring are produced as the organism grows).

? How might groups of genetically identical individuals be identified in clones that form by budding? By apomixis? By horizontal spread?

CONCEPT 9.2
The distributions and abundances of organisms are limited by habitat suitability, historical factors, and dispersal.

Distribution and Abundance

Many different factors can influence the distributions and abundances of organisms. We'll survey these factors by grouping them into three categories: habitat suitability, historical factors (such as evolutionary history and continental drift), and dispersal.

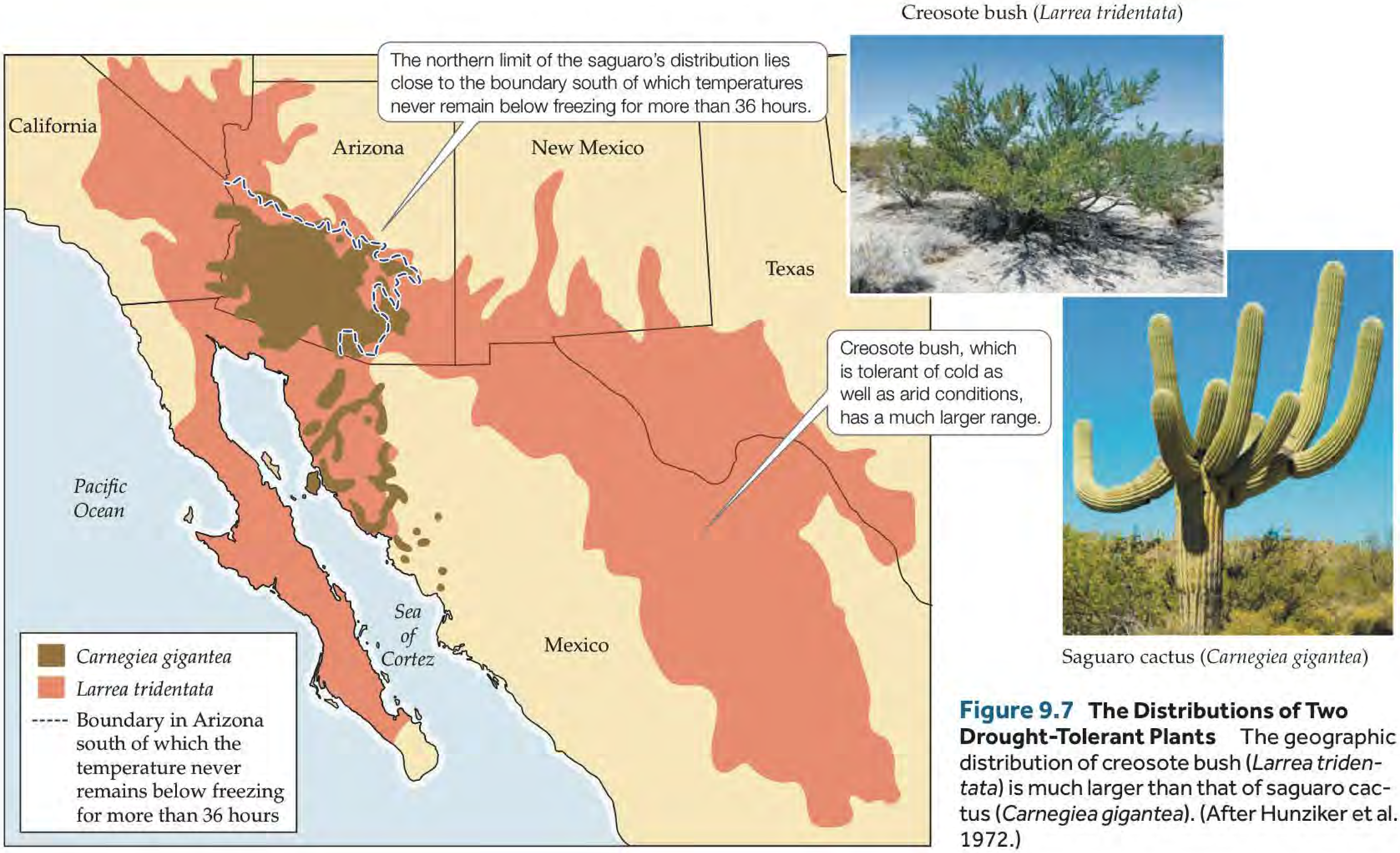
Habitat suitability limits distribution and abundance

Good and poor places to live exist for all species. A desert species is not likely to perform well in the Arctic, or vice versa. Even small differences among environments in how well individuals survive or reproduce there can cause the abundance of a species to be high in certain environments and low in others. Thus, the distribution and abundance of a species are influenced strongly by the presence of suitable habitat. But what factors make habitat suitable?

ABIOTIC FEATURES OF THE ENVIRONMENT As we discussed in Unit 1, the climate and other aspects of the abiotic (nonliving) environment, such as soil pH, salt concentration, and available nutrients, set limits on whether a habitat will be suitable for a particular species. Some species can tolerate a broad range of physical conditions, while others have more narrow requirements.

Creosote bush (*Larrea tridentata*), for example, has a broad distribution in North American deserts, ranging across much of the southwestern United States and northwestern and central Mexico (**Figure 9.7**). Creosote bush is very tolerant of arid conditions: it uses water rapidly when it is available, then shuts down its metabolic processes during periods of extended drought. Creosote bush also tolerates cold well, so its populations thrive in high-elevation deserts where winter temperatures can remain below freezing for several days.

The saguaro cactus (*Carnegiea gigantea*), on the other hand, has a more limited distribution. Like creosote bush, saguaro flourishes under arid conditions, but it achieves its drought tolerance in different ways. Although saguaro does not have typical leaves, its spines are actually modified leaves whose low surface area reduces water loss.



Creosote bush (*Larrea tridentata*)

Saguaro cactus (*Carnegiea gigantea*)

Figure 9.7 The Distributions of Two Drought-Tolerant Plants The geographic distribution of creosote bush (*Larrea tridentata*) is much larger than that of saguaro cactus (*Carnegiea gigantea*). (After Hunziker et al. 1972.)

Furthermore, during wet periods, saguaro stores water in its massive trunk and arms, saving it for use during times of drought. Saguaro cannot tolerate cold, however; it is killed when temperatures remain below freezing for 36 hours or more. The importance of saguaro's sensitivity to cold is revealed by its distribution: the northern limit of its distribution corresponds closely to a boundary north of which temperatures occasionally remain below freezing for at least 36 hours (see Figure 9.7).

BIOTIC FEATURES OF THE ENVIRONMENT The biotic environment also has important effects on distributions and abundances of species. Obviously, species that depend completely on one or a few other species for their growth, reproduction, or survival cannot live where the species on which they depend are absent. Organisms can also be excluded from an area by herbivores, predators, competitors, parasites, or pathogens, any of which can greatly reduce the survival or reproduction of members of a population.

A dramatic example of such exclusion is provided by the successful biological control of *Opuntia stricta*, an introduced cactus that spread rapidly to cover large areas in Queensland and New South Wales, Australia. The cactus was imported from the southern United States in 1839 and planted as hedge. Within 40 years, *O. stricta* had become a pest species, and by 1925 it covered 243,000 km^2. The cactus can grow up to 2 m high, and in many areas it covered the ground with dense, spiny thickets, making the rangelands it occupied useless (**Figure 9.8A**). In the hope of controlling the cactus, an Argentinean moth, *Cactoblastis cactorum*, known to feed on *Opuntia* was released in 1926 (**Figure 9.8B**). By 1931, the moths had spread widely and destroyed billions of cacti. Since 1940, the cactus has persisted in small numbers, but its distribution and abundance have been greatly reduced. Although the introduction of *C. cactorum* as a means of biological pest control appears to have been a great success, such introductions must be undertaken cautiously because they can lead to unintended consequences, such as damage to native species (Louda et al. 1997).

INTERACTIONS BETWEEN ABIOTIC AND BIOTIC FEATURES In many cases, abiotic and biotic features of the environment act together to determine the distribution and abundance of a species. For example, the barnacle *Semibalanus balanoides* cannot survive where summer air temperatures are above 25°C, and it cannot reproduce if winter air temperatures do not remain below 10°C for 20 days or more. On the Pacific coast of North America, temperatures are such that *S. balanoides* could be found 1,600 km farther south than it currently is. But this barnacle is absent from the region shown in purple in **Figure 9.9**, presumably because competition from other species of barnacles prevents it from living in what would otherwise be suitable habitat. To the north, as temperatures become increasingly colder, a point is reached where *S. balanoides* outcompetes the other barnacles and maintains healthy populations. Thus, the abiotic and biotic environments interact to determine where populations of this barnacle are found.

DISTURBANCE The distributions of some organisms depend on regular forms of disturbance. A **disturbance** is an abiotic event that kills or damages some individuals and thereby creates opportunities for other individuals to grow and reproduce. Many plant species, for example, persist in an area only if there are periodic fires. If humans prevent fires, such species are replaced by other species that are not as tolerant of fires but are superior competitors in the absence of fires. Thus, a change in the frequency of fires can change the composition of ecological communities, as you can explore in **Analyzing Data 9.1**. Floods, windstorms, and droughts are other forms of disturbance that can harm some species but give others an advantage. We'll discuss the role of disturbance in more detail in Chapter 17.

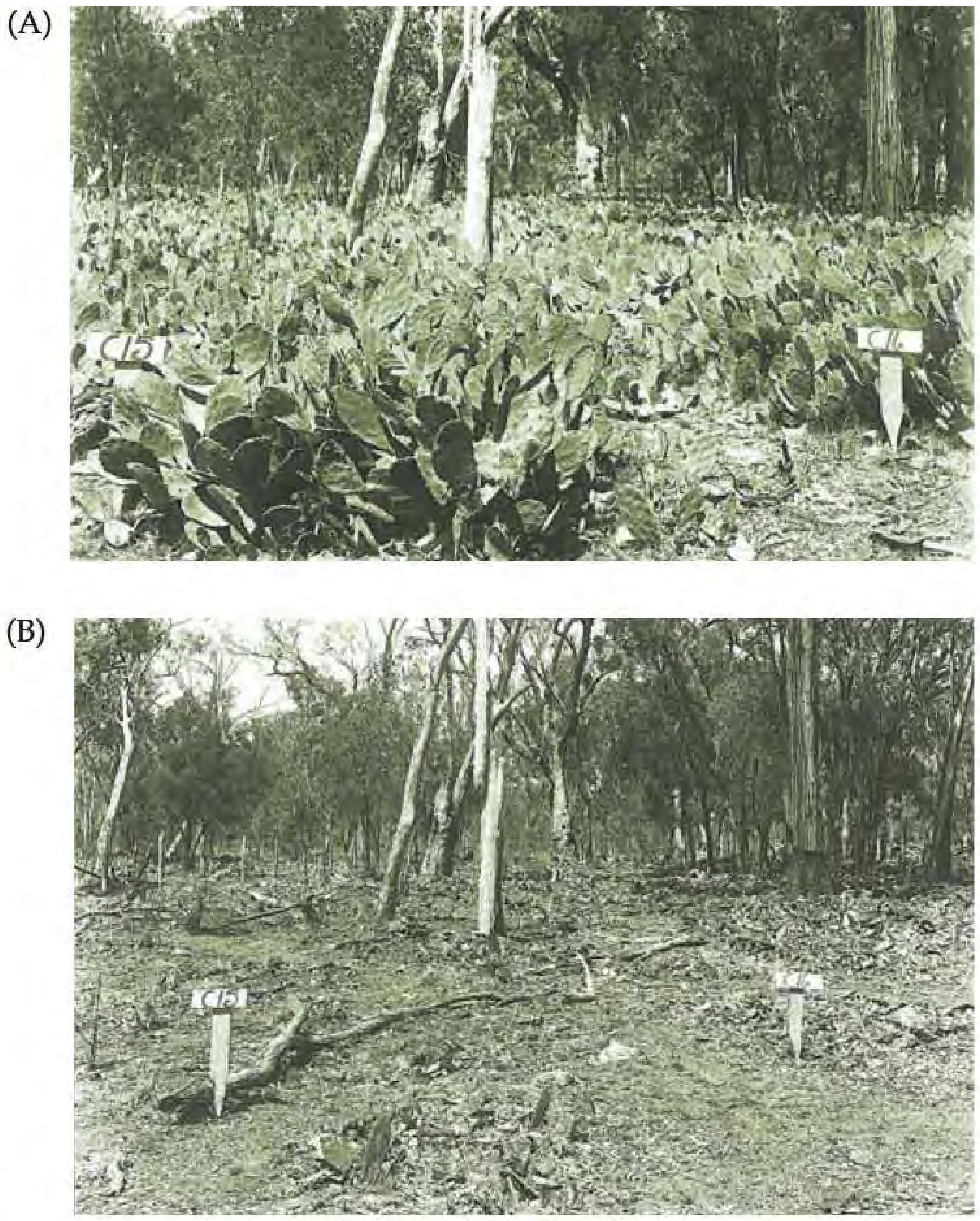
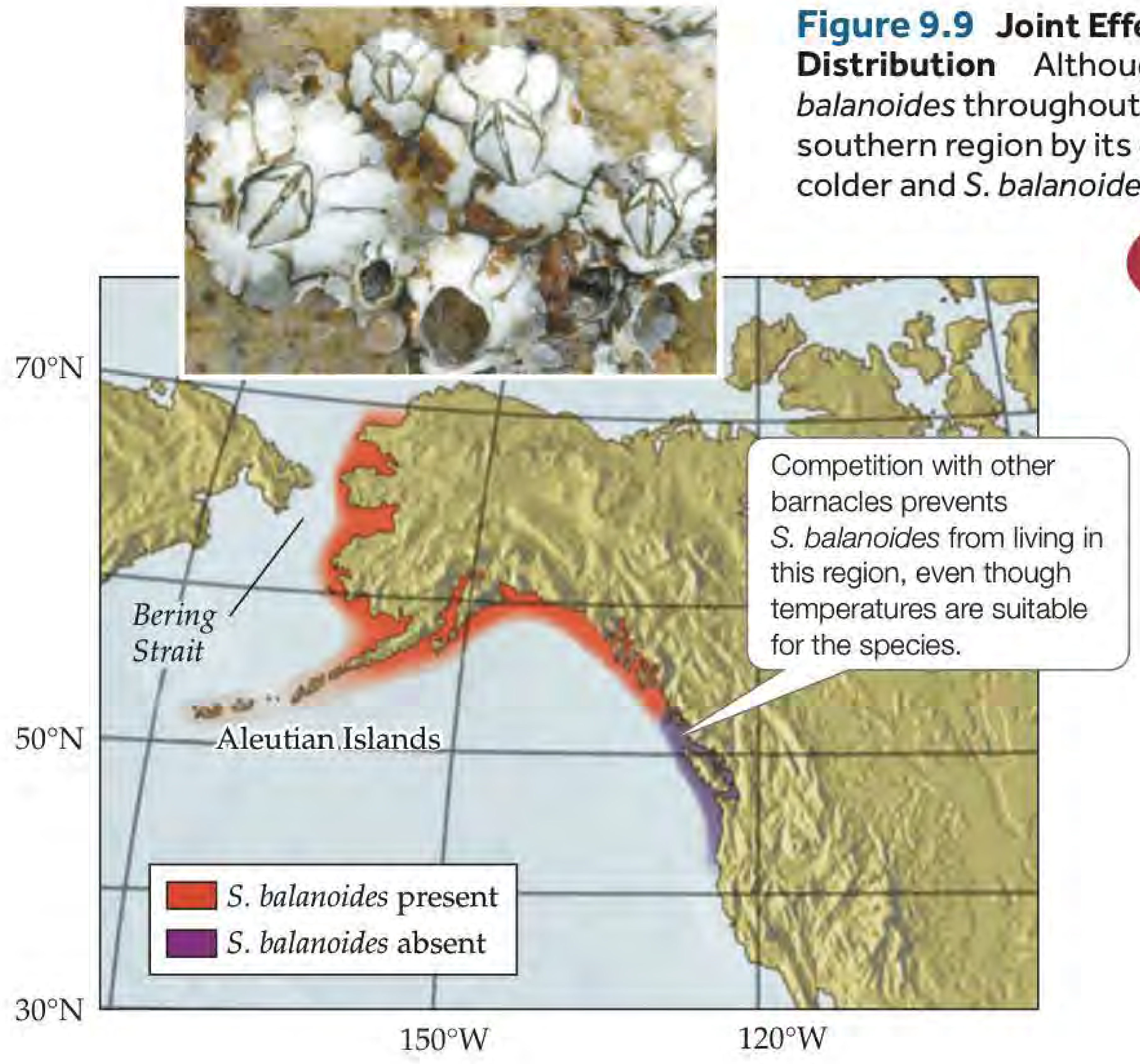


Figure 9.8 Herbivores Can Limit Plant Distributions In Australia, the moth *Cactoblastis cactorum* was used to control populations of an introduced cactus, *Opuntia stricta*. (A) A dense thicket of *O. stricta* 2 months before the release of the moth. (B) The same stand 3 years later, after the moth had killed the cacti by feeding on their growing tips. (From Department of Natural Resources, Queensland, Australia.)



Competition with other barnacles prevents *S. balanoides* from living in this region, even though temperatures are suitable for the species.

Figure 9.9 Joint Effects of Temperature and Competition on Barnacle Distribution Although temperatures are suitable for the barnacle *Semibalanus balanoides* throughout the red- and purple-shaded regions, it is excluded from the southern region by its competitors. In the red-shaded regions, temperatures are colder and *S. balanoides* is the superior competitor.

? Is global warming likely to increase or decrease the geographic range of *S. balanoides*? Explain.

History and dispersal limit distribution and abundance

Species can persist only in regions of suitable habitat, but they are not found in all such places. History and dispersal also play important roles in their distributions and abundances.

EVOLUTIONARY AND GEOLOGIC HISTORY Events in the evolutionary and geologic history of Earth have had a profound effect on where organisms live today. Why, for example, are polar bears (*Ursus maritimus*) found in the Arctic but not in Antarctica? Polar bears hunt on ice packs and eat seals, both of which abound in Antarctica. Part of the answer to our question can be found in the evolutionary history of these bears. Fossil and genetic evidence indicate that polar bears evolved from brown bears (*Ursus arctos*) in the Arctic (Lindqvist et al. 2010);

ANALYZING DATA 9.1 Have Introduced Grasses Altered the Occurrence of Fires in Hawaiian Dry Forests?

Bush beardgrass (*Schizachyrium condensatum*), molasses grass (*Melinis minutiflora*), and several other non-native grasses were introduced by humans to Hawaii as forage for livestock. By 1969, introduced grasses had invaded the dry forests of Volcanoes National Park, Hawaii. These dry forests are open woodlands with an understory of shrubs; they contain few or no native grasses. Hughes et al. (1991)* provide data on fire occurrence (**Table A**) and on vegetation abundance in unburned and burned regions of dry forests in the park (**Table B**).

1. Using the data in Table A, calculate the frequency of fires and the average area burned before and after introduced grasses invaded Volcanoes National Park. What do your results suggest about how introduced grasses have affected the occurrence of fires in Volcanoes National Park?
2. Based on the data in Table B, does fire promote or limit the abundance of native trees and shrubs? How does fire affect introduced grasses?
3. Introduced grasses recover quickly from fires, and they provide more fuel for future fires than do native trees and shrubs. Use this information to predict what may happen if a fire occurs in a Hawaiian dry forest after introduced grasses have invaded that forest. Do the events you've described help to explain the data in Tables A and B? Explain your reasoning.

Table A

TIME FRAME	NUMBER OF FIRES	TOTAL AREA BURNED
1928–1968	9	2.3 ha
1969–1988	32	7,800 ha

Table B

	VEGETATION ABUNDANCE INDEX		
VEGETATION TYPE	UNBURNED	BURNED ONCE	BURNED TWICE
Native trees and shrubs	112.3	5.2	0.7
Introduced grasses	80.0	92.1	100.9

See the companion website for a similar ANALYZING DATA exercise.

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*Hughes, F., P. M. Vitousek and T. Tunison. 1991. Alien grass invasion and fire in the seasonal submontane zone of Hawai'i. *Ecology* 72: 743–746.

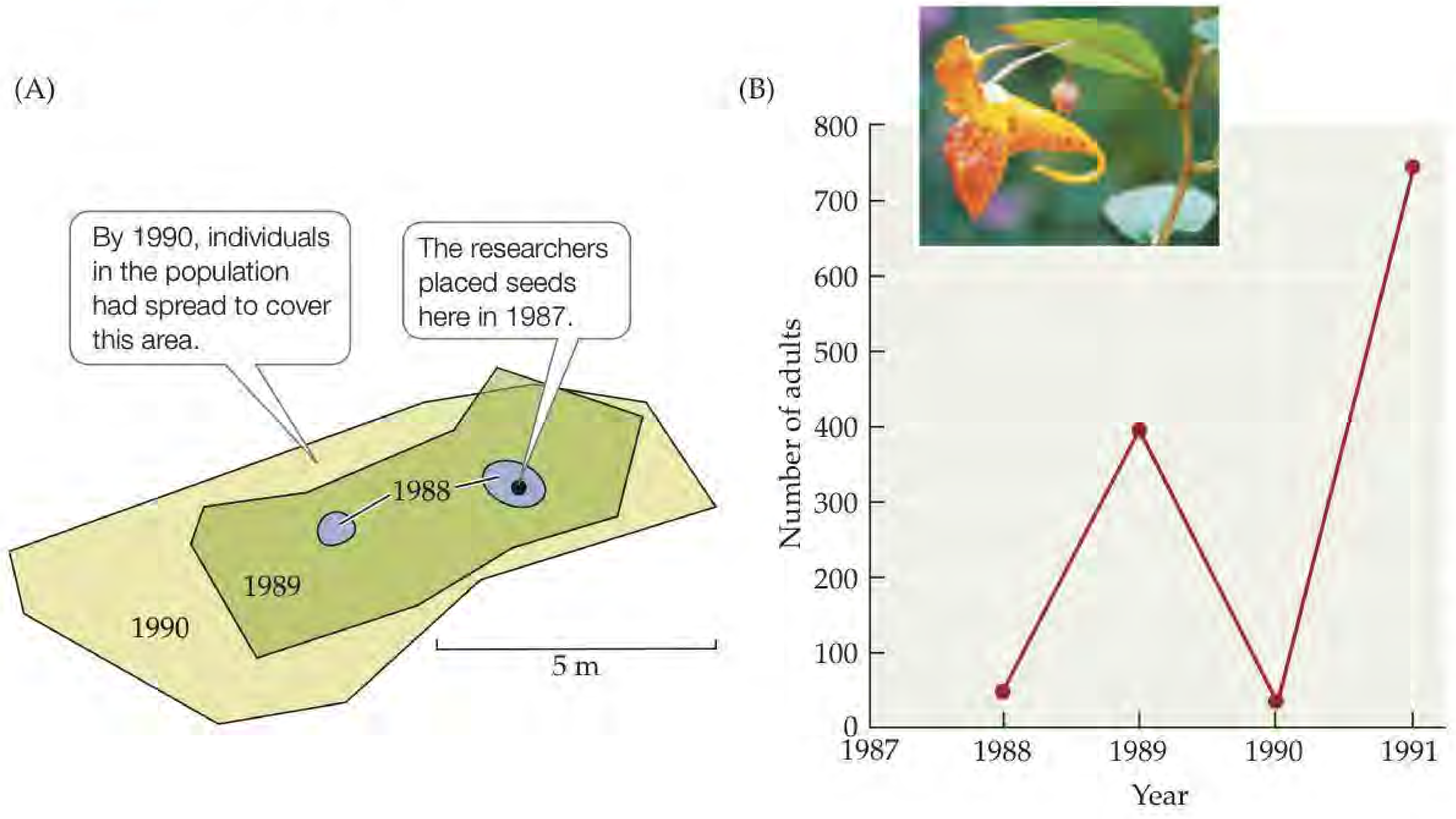


Figure 9.10 Populations Can Expand after Experimental Dispersal An experiment demonstrated that dispersal limitation had prevented established populations of *Impatiens capensis* from colonizing nearby areas where the plant could grow. (A) In 1987, 100 seeds from an established population located 75 m away were scattered within 1 m of the black dot. The map shows the distribution of the population in the years 1988–1990; the distribution for 1991 was not mapped. (B) The graph shows the number of adults in the population in the years 1988–1991. Note that although the abundance dropped in 1990, some individuals had spread far enough that the population covered the larger area shown in part A. (After Primack and Miao 1992.)

hence *U. maritimus* is found in the Arctic because the species originated there. As for their absence from Antarctica, although polar bears can travel over 1,000 km in a year, it appears they cannot or will not cross the tropical regions that separate the Arctic from Antarctica. Thus, the distribution of polar bear populations is influenced by evolutionary history and dispersal as well as by the presence of suitable habitat.

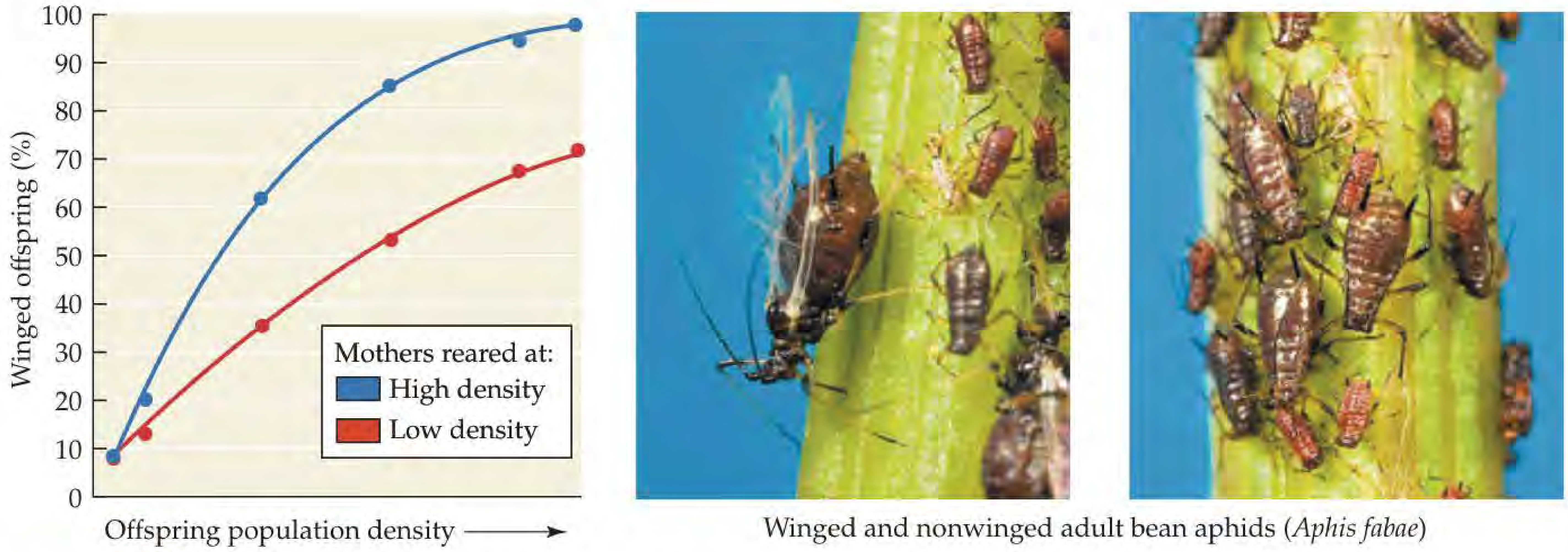
Geologic history plays a key role in some curious distribution patterns that puzzled biologists for nearly 100 years. Consider Alfred Russel Wallace's observation that the animals of a region can differ considerably across relatively short geographic distances (Wallace 1860). The mammal communities of the Philippines, for example, are more similar to those in Africa (88% overlap at the family level) than they are to those in New Guinea (64% overlap), despite the fact that Africa is 5,500 km away and New Guinea is only 750 km away. No explanation for this and other similar observations could be found until the discovery of *continental drift*, the gradual movement of continents over time (see Web Extension 18.1). This discovery led to the realization that the Philippines and New Guinea are on different tectonic plates and have been in close geographic contact for a relatively short time.

DISPERSAL LIMITATION As demonstrated by the polar bear's absence from Antarctica, a species' limited capacity for dispersal can prevent it from reaching areas of suitable habitat—a phenomenon known as **dispersal limitation**. In another example, the Hawaiian Islands have only one native terrestrial mammal, the Hawaiian hoary bat (*Lasiurus cinereus*), which was able to fly to the islands. No other land mammals have been able to disperse to Hawaii on their own, although cats, pigs, wild dogs, rats, goats, mongooses, and other mammals now thrive in Hawaii following their introduction to the islands by people.

Dispersal limitation can also occur on smaller spatial scales, preventing populations from expanding to nearby areas of apparently suitable habitat. Primack and Miao (1992) documented such local dispersal limitation in the herbaceous plant *Impatiens capensis* (**Figure 9.10**). Similar results were obtained in a long-term study of the English bluebell (*Hyacinthoides non-scripta*). In 1960, 27 populations of 7–10 individuals each were established in apparently suitable forest habitat located near source populations (Van der Veken et al. 2007). Forty-five years later, 11 (41%) of these experimental populations persisted, and most contained hundreds or thousands of individuals. These results suggested that dispersal limitation had prevented the bluebells from reaching habitat where they could thrive.

DISPERSAL AND DENSITY When individuals disperse from one population to another, the density of the population they leave decreases and the density of the population they join increases. Dispersal can also be affected *by* population density. For example, many species of aphids produce winged forms (which are capable of dispersing) in response to crowding (Harrison 1980). This point is illustrated by the bean aphid (*Aphis fabae*), in which the percentage of offspring that develop wings increases as the density of aphids increases (**Figure 9.11**).

Density and dispersal may play similar roles in populations of the desert pupfish (*Cyprinodon macularius*) (**Figure 9.12**). Following heavy rains, the pools in which these fish live are connected to one another by temporary streams. Dispersal is risky for fish that live in desert pools, but under certain circumstances, it can be advantageous. As explored in **Web Extension 9.1**, results from

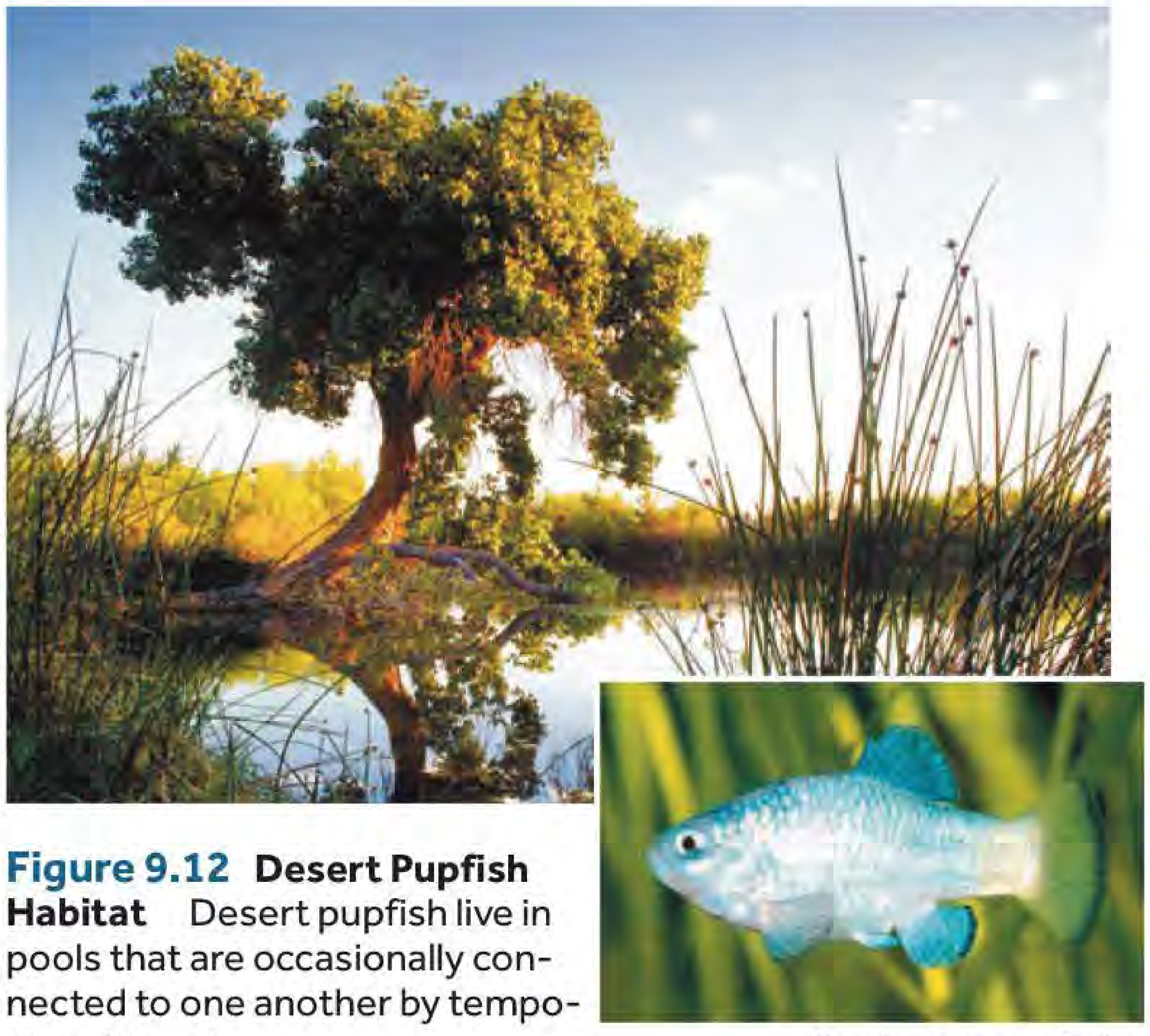


Winged and nonwinged adult bean aphids (*Aphis fabae*)

Figure 9.11 Density Can Affect Dispersal The proportion of aphid offspring that develop wings in relation to the density at which they were reared, for mothers who were themselves reared at high or low densities. (After Shaw 1970.)

? Do the results shown in the graph indicate that aphids are more likely to develop wings in response to high densities experienced by the offspring, by their mothers, or both? Explain.

experiments on desert pupfish suggest that dispersal may provide them with a greater chance for survival and reproduction than they would have if they remained in crowded pools with limited food (McMahon and Tash 1988). Many other organisms alter their rates of dispersal in response to conditions that affect survival and reproduction, such as increases in the abundance of predators or competitors, or decreases in habitat quality or the availability of mates (Poethke et al. 2010).



Cyprinodon macularius

Figure 9.12 Desert Pupfish Habitat Desert pupfish live in pools that are occasionally connected to one another by temporary streams.

CONCEPT 9.3

Many species have a patchy distribution of populations across their geographic range.

Geographic Range

As we saw in the previous section, the distribution of a species can be affected by the presence of suitable habitat, geologic and evolutionary history, and dispersal. In many cases, we expect that several or perhaps all of these factors will operate at the same time to influence where a species is found. The net effect of these interacting factors limits some species to a small geographic region, while other species have much larger distributions. But whether a species inhabits a small or a large geographic area, no species can live everywhere, since much of Earth consists of unsuitable habitat for its populations.

Geographic ranges vary in size among species

The **geographic range** of a species is the entire geographic region over which that species is found. Although there are no species that are found everywhere, there is considerable variation in the sizes of their geographic ranges. Examples of species with small geographic ranges include the Devil's Hole pupfish (*Cyprinodon diabolis*), which lives in a single desert pool (7 × 3 m across and 15 m deep). Many tropical plants also have small geographic ranges. This latter point was illustrated dramatically in 1978, when 90 new plant species were discovered on a single mountain ridge in Ecuador, each with a geographic range that was restricted to that ridge. Other species, such as coyotes, live over most of one continent (North America), while still others, such as gray wolves, live on small portions of several continents (North America and Eurasia). Relatively few terrestrial species are found on all or most of the world's continents. Notable exceptions include humans, Norway rats, and the bacterium *Escherichia coli*, which lives in the intestinal tracts of reptiles, birds, and mammals (including humans) and thus is found wherever its host organisms are found. Some marine species, including invertebrates with planktonic larvae (see Figure 7.11) and whales, have large geographic ranges. But while range sizes vary greatly, the pattern in the oceans is similar to that on land, and for most marine species the geographic range is relatively small (Gaston 2003).

The geographic range of a species includes the areas it occupies during all of its life stages. It is particularly important to keep this fact in mind for species that migrate and for species whose biology is poorly understood. For example, if we wish to protect monarch butterfly populations, we must ensure that conditions are favorable for them in both their summer breeding grounds and their overwintering sites. In some cases, we understand an organism's range poorly because it has life stages that are hard to find or study; this is true of many fungi, plants, and insects. We may know under what conditions the adult organism lives, yet have no idea where or how other life stages live. In fact, that was long the case for the monarch butterfly. Biologists knew that each spring these butterflies arrived in eastern North America from the south, but it took almost 120 years (from 1857 to 1975) before their overwintering sites were discovered in mountains west of Mexico City.

Populations have patchy distributions

Even within the geographic range of a species, much of the habitat is not suitable for the species. As a result, populations tend to have a patchy distribution. This observation holds at both large and small spatial scales. On land, for example, at the largest spatial scales, climate constrains where populations of a species are located (see Concept 3.1). At smaller spatial scales, factors such as topography, soil type, and the presence or absence of other species prevent populations from being spread evenly across the landscape.

A vivid example of patchiness at different spatial scales is provided by work Ralph Erickson performed on the herbaceous perennial *Clematis fremontii* (**Figure 9.13**). This species is found in portions of Kansas, Nebraska, and Missouri. Erickson studied the distribution of *C. fremontii* in Missouri, where it is found in a small region in the eastern part of the state and is restricted to areas of dry, rocky soil that support few trees in otherwise wooded areas; such areas are called *barrens* or *glades*. The glades on which *C. fremontii* is found occur on outcrops of limestone located on south- or west-facing slopes. As shown in Figure 9.13, these glades are clustered, or grouped in clumps, when viewed across the range of the species in eastern Missouri. The distribution of glades remains clustered at progressively smaller scales as well. Individual plants are also found in clusters, both as groups of individuals within a glade and as aggregates of individuals within one of these groups.

Clematis fremontii requires a very particular habitat that is found only in portions of its geographic range; hence its populations have a highly patchy distribution.

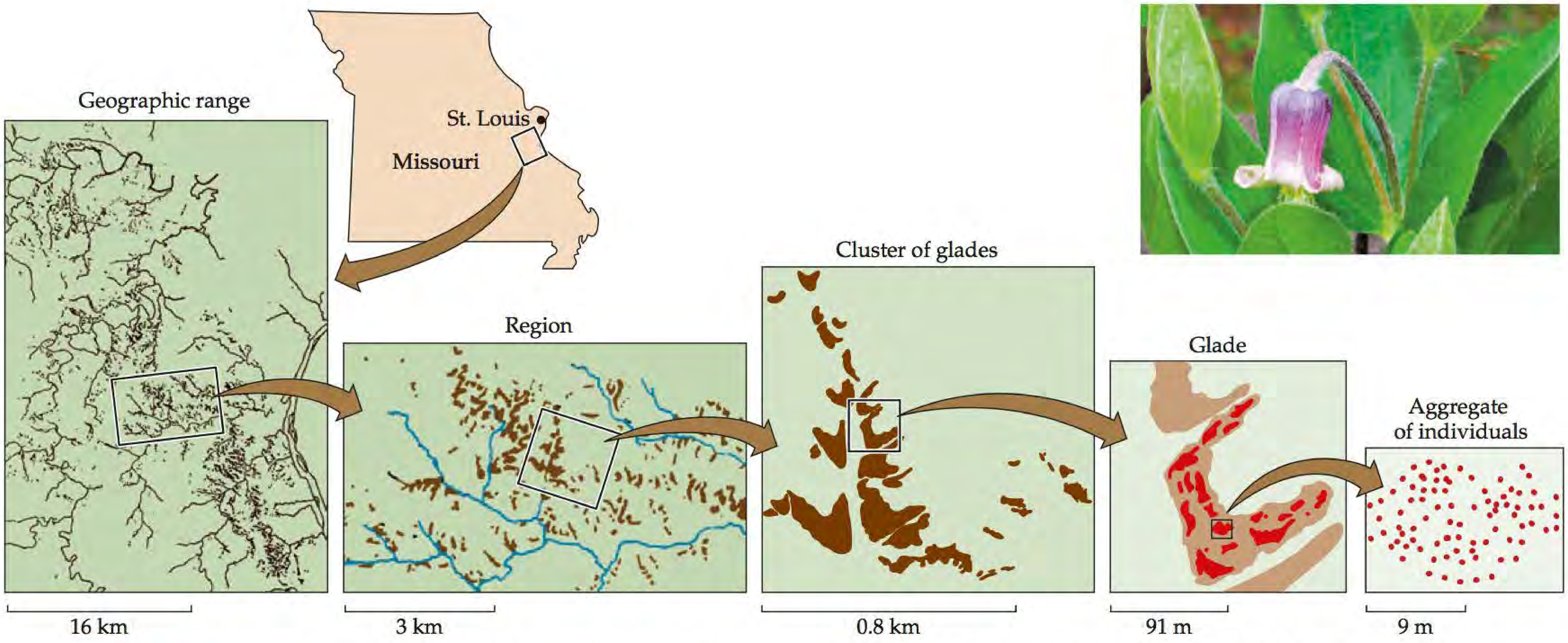
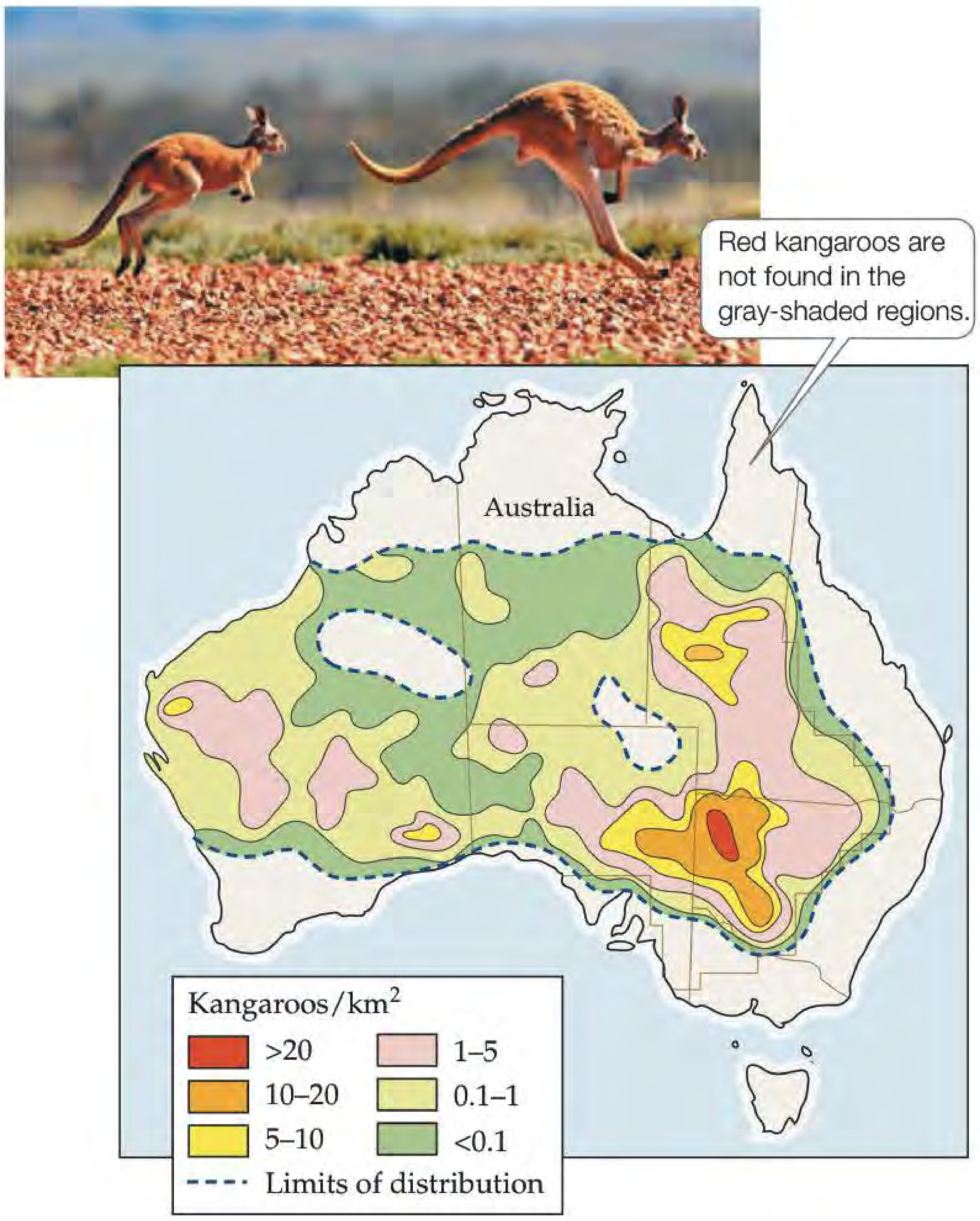


Figure 9.13 Many Populations Have a Patchy Distribution At various scales of observation—from its geographic range in Missouri to aggregates of individuals within a glade—populations of the herbaceous plant *Clematis fremontii* have a patchy distribution. The patchy distribution of this plant is controlled largely by the patchy distribution of suitable habitat. (After Erickson 1945; photo courtesy of J. Trager.)

Other species tolerate a broader range of habitats, but their abundances still vary throughout their geographic range. The distribution of red kangaroos (*Macropus rufus*) in arid regions of Australia illustrates this point. The abundance of red kangaroos varies throughout their geographic range, which includes several regions of high density and several areas where red kangaroos are not found (**Figure 9.14**).

Next we turn to factors that influence the location of individuals within populations.



Red kangaroos are not found in the gray-shaded regions.

Figure 9.14 Abundance Varies throughout the Geographic Range of a Species The map shows abundances of the red kangaroo (*Macropus rufus*) throughout its range in Australia. These data were based on aerial surveys conducted from 1980 to 1982. (After Caughley et al. 1987.)

CONCEPT 9.4

The dispersion of individuals within a population depends on the location of essential resources, competition, dispersal, and behavioral interactions.

Dispersion within Populations

The aggregates of *Clematis fremontii* individuals found in glades provide an example of the **dispersion**, or spatial arrangement, of individuals within a population. We can recognize three basic patterns in how the individuals of a population are positioned with respect to one another (**Figure 9.15**). In some cases, the members of a population have a **regular dispersion**, in which individuals are relatively evenly spaced throughout their habitat. In other cases, individuals show a **random dispersion**, similar to what would occur if individuals were positioned at locations selected at random. Finally, as in *C. fremontii*, individuals may be grouped together to form a **clumped dispersion**. In natural

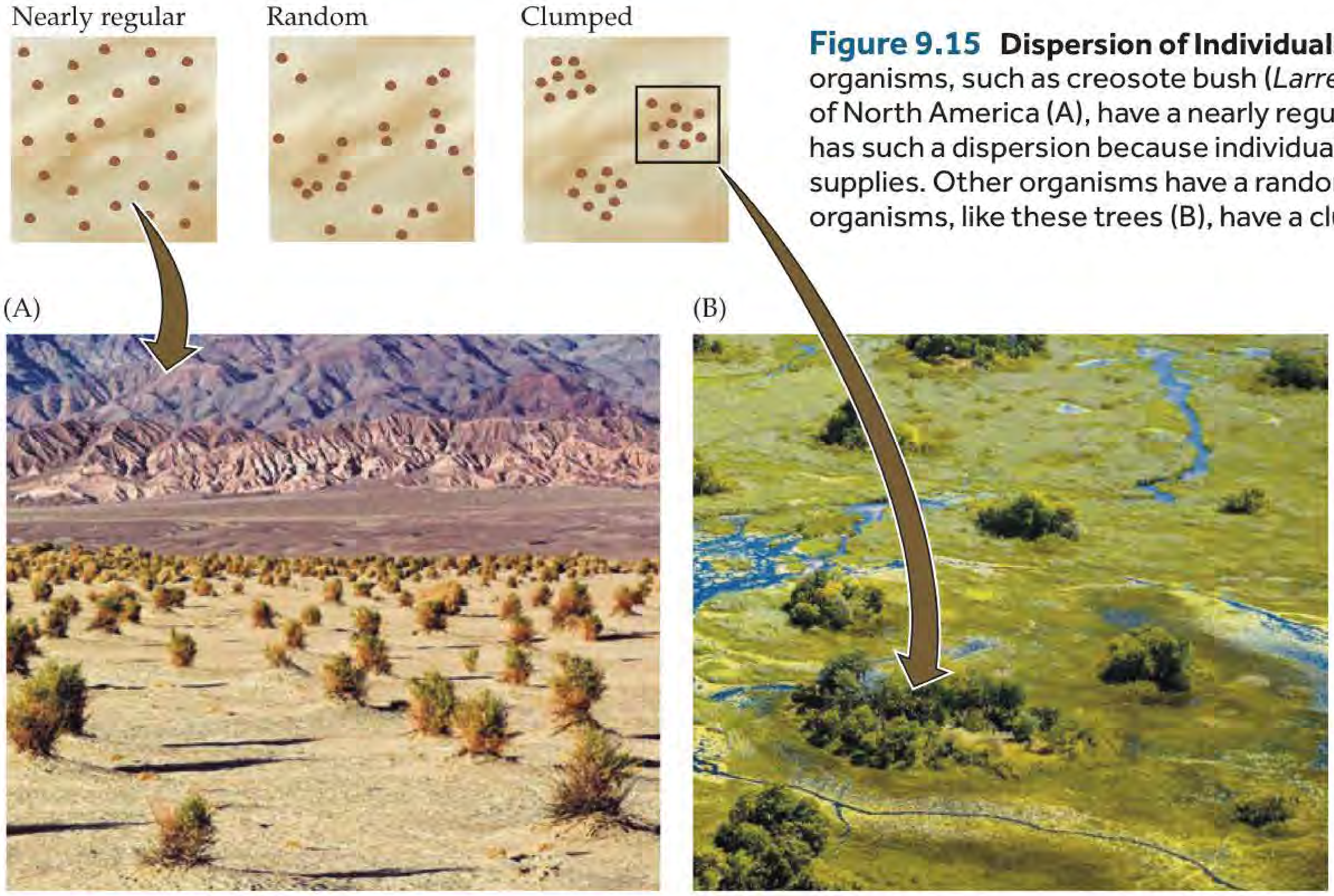


Figure 9.15 Dispersion of Individuals within Populations Some organisms, such as creosote bush (*Larrea tridentata*) in the Mojave Desert of North America (A), have a nearly regular dispersion. Creosote probably has such a dispersion because individual plants compete for limited water supplies. Other organisms have a random dispersion, and the majority of organisms, like these trees (B), have a clumped dispersion.

populations, clumped dispersions are more common than either regular or random dispersions.

Resources, competition, and dispersal affect dispersion within populations

A variety of processes can cause individuals to have a regular, random, or clumped dispersion. Consider a plant that grows poorly unless particular resources and environmental conditions are all present (e.g., the right combination of soil nutrients, light, and temperature). In such a case, the spatial arrangement of individuals within a population would be likely to match the spatial arrangement of conditions suitable for growth. Since environmental conditions often vary at random or are clumped in space, our hypothetical plant might be expected to have a random or clumped dispersion. Random or clumped dispersions can also occur as a result of dispersal; for example, short dispersal distances can cause individuals to clump together. In some instances, competition for resources or space appears to have resulted in a nearly regular dispersion, as has been observed for the creosote bushes shown in Figure 9.15A.

Individual behavior affects dispersion within populations

Interactions among individual organisms also influence dispersion patterns. Individuals may repel one another (to produce nearly regular dispersions) or attract one another (to produce clumped dispersions). Both of these tendencies can be seen in the Seychelles warbler (*Acrocephalus sechellensis*), an endangered songbird. In the 1950s, this bird nearly went extinct: its total world population was reduced to just 26 individuals located on Cousin Island in the Seychelles, a group of islands off the east coast of Africa. After the Seychelles warbler was legally protected in 1968, the Cousin Island population increased to about 300 birds, and the species was introduced successfully to two other islands.

Seychelles warblers are territorial: a breeding pair defends its territory against other birds of the species. This behavior causes the dispersion of individuals in the population to be somewhat regular (**Figure 9.16**). But not all territories are equal: some are of higher quality than others because they provide more food (e.g., insects). Birds that live in a high-quality territory live longer and produce more young. In addition, a breeding pair that lives in a high-quality territory often receives help rearing its young from offspring born in previous years. Because the high-quality sites attract offspring from previous years and are aggregated toward one end of the island, differences in territory quality make the dispersion of individuals in the population more clumped than it otherwise would be.

As we've seen, population sizes often vary greatly at a number of scales over time and space. Thus, a key challenge in studying a population is estimating its abundance.

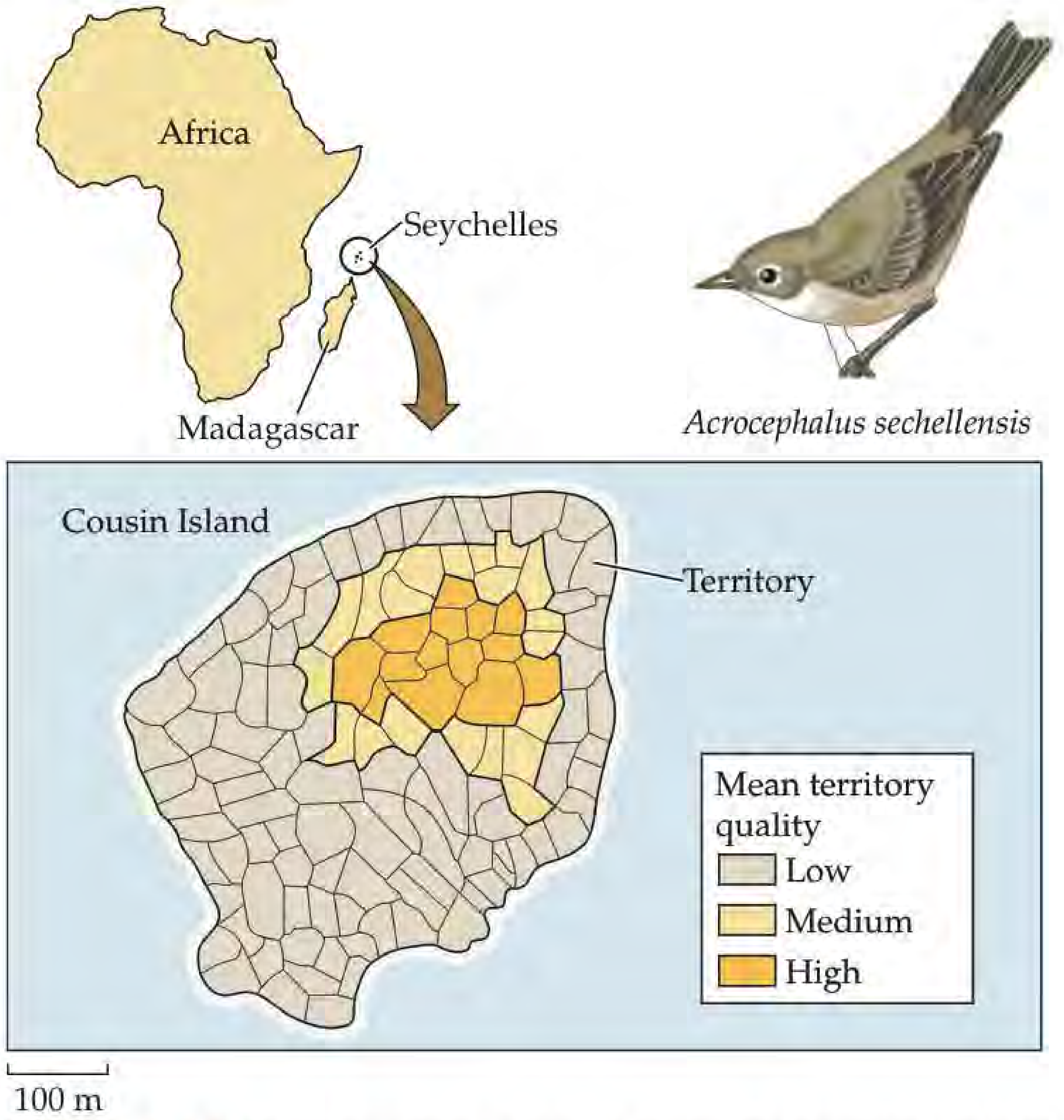


Figure 9.16 Territorial Behavior Affects Dispersion within Populations The mean quality of Seychelles warbler territories on Cousin Island across the years 1986 to 1990. Territories were grouped into three quality categories: high, medium, and low. High-quality territories were clustered inland; these territories had high vegetation cover, little wind, and abundant insects. Coastal areas had lower-quality territories because salt spray led to defoliation, which lowered insect abundance. (After Komdeur 1992.)

CONCEPT 9.5

Population abundances and distributions can be estimated with area-based counts, distance methods, mark–recapture studies, and niche models.

Estimating Abundances and Distributions

The most direct way to determine how many individuals live in a population is to count all of them. This sounds simple enough, and it is possible in some cases, as for the Seychelles warblers on Cousin Island, the *Clematis fremontii* in a Missouri glade, and other organisms that are confined to small areas, are easy to see, or do not move. But complete counts of organisms are often difficult or impossible. Consider the chinch bug (*Blissus leucopterus*), an insect that attacks crops such as corn and wheat. This insect can cover large areas and reach densities that exceed 5,000 individuals per square meter, making it impractical to count all the individuals in a population. In such cases, a variety of methods can be used to estimate abundance.

Ecologists estimate abundance with area-based counts, distance methods, and mark–recapture studies

Many ecological studies require an estimate of a population's actual abundance, or **absolute population size**. For example, to quantify the extent to which the number of wolves affects and is affected by the number of their elk prey, we must estimate the absolute population sizes of both species. In other cases, it may be sufficient to estimate the **relative population size**, the number of individuals in one time interval or place *relative to* the number in another. Estimates of relative population size are based on data that are presumed to be correlated with absolute population size but do not assess the actual number of individuals in the population. Examples of such data include the number of cougar tracks found in an area, the number of fish caught per unit of effort (e.g., per number of hooks trolled each day), or the number of birds observed while the observer walks a standard distance (or remains in one place for a standard time interval).

Relative population size estimates are usually easier and less expensive to obtain than are absolute estimates. While useful, estimates of relative population size must be interpreted carefully. The number of cougar tracks observed, for example, depends not only on cougar population density, but also on animal activity. Thus, if twice as many tracks were found in area A as in area B, we could not be confident that area A had twice as many cougars—there could be more or fewer than that, depending on whether cougars moved more frequently in one area than in another.

With the distinction between absolute and relative population size as background, we turn now to how ecologists estimate abundance. In **Ecological Toolkit 9.1**, we describe three common approaches: area-based counts, distance methods, and mark–recapture studies.

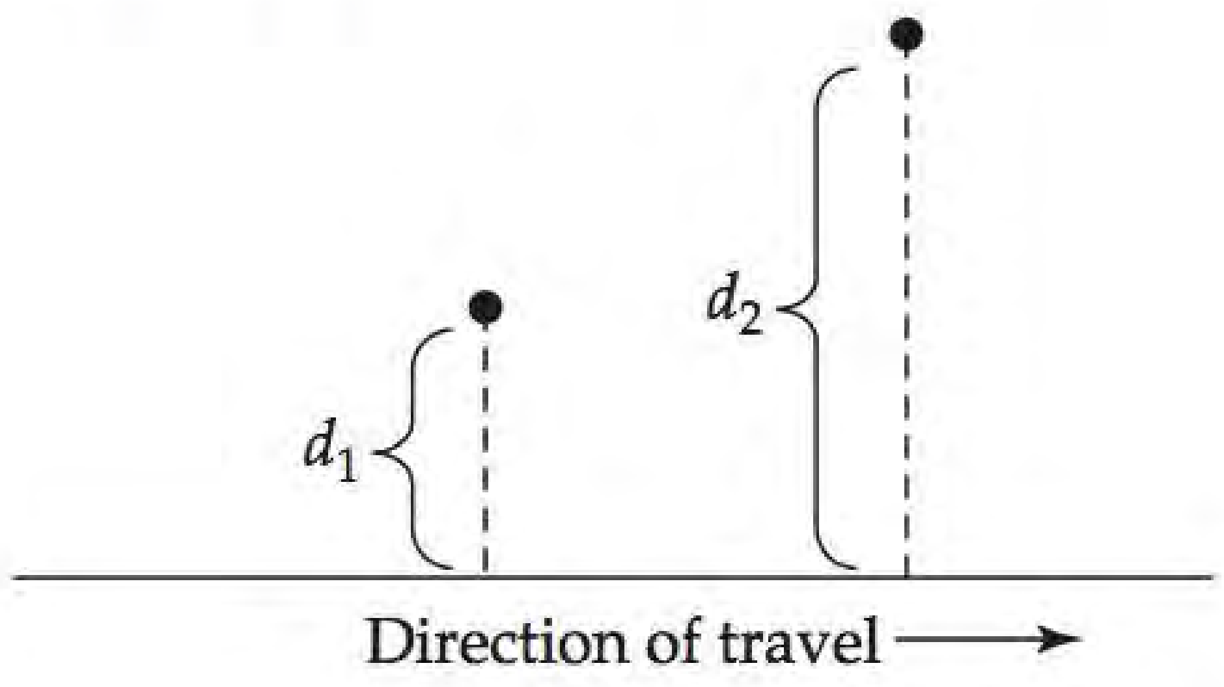
AREA-BASED COUNTS As described in Ecological Toolkit 9.1A, area-based counts are often used to estimate the population sizes of immobile organisms. In this approach, organisms are counted in a series of sample plots, or quadrats, and the resulting numbers are used to estimate the total population size. Suppose, for example, that a team of entomologists wants to estimate the population of chinch bugs in a 400 ha (ca. 1,000-acre) field of corn. If they counted chinch bugs in five 10 cm × 10 cm quadrats (i.e., five 0.01 m^2 quadrats), and their counts were 40, 10, 70, 80, and 50 chinch bugs, they would estimate that there were, on average,

$$\frac{(40+10+70+80+50)/5}{0.01}=5{,}000 \qquad \textbf{(9.1)}$$

chinch bugs per square meter. Thus, there would be an estimated 20 billion chinch bugs in the population (5,000 bugs/m^2 × 10,000 m^2/ha × 400 ha = 20,000,000).

Area-based methods work well if individuals can be counted accurately within the quadrats, and if the quadrats provide a good representation of the entire area covered by the population. To help ensure that the latter condition is met, ecologists use as many quadrats as is feasible, and they often place those quadrats at locations selected at random from the entire area covered by the population. Quadrats can also be placed in a variety of other ways, such as at evenly spaced locations along a rectangular grid.

DISTANCE METHODS Estimates of abundance can also be based on various measurements of distance from a point or line. Such distance methods are "plotless" in that they are not made by counting individuals located within a given area or volume. For example, in the **line transect** approach, an observer travels by foot, horseback, or vehicle along a transect line:



Each individual that the observer can see from the line is counted, and its perpendicular distance from the line is recorded (d_1 and d_2 in the above example). As described in Ecological Toolkit 9.1B, a *detection function* must be used to convert such distance measurements into an estimate of the absolute population size.

MARK–RECAPTURE STUDIES The mark–recapture approach relies on releasing marked individuals and then recapturing them at a later time to see what fraction of the population is marked (see Ecological Toolkit 9.1C). Imagine, for example, that we capture 23 butterflies from a meadow, which we then mark and release. A day later, we sample the meadow again, this time catching 15 butterflies, of which 4 are marked. In our first sample, we caught and marked $M_1 = 23$ butterflies from a total population of unknown size (N); thus, we initially caught a proportion M_1/N of the butterflies in the field. The second time butterflies were sampled, we caught $M_2 = 15$ butterflies, of which 4 were marked and hence were recaptured ($R = 4$).

Assuming that no butterfly births, deaths, or movements into or out of the meadow have occurred since our first sample, the proportion of marked individuals captured in our second sample (R/M_2) should equal the

ECOLOGICAL TOOLKIT 9.1 Estimating Abundance

Methods for estimating abundance fall into three general categories: area-based counts, distance methods, and mark–recapture studies. Many variations on these approaches have been developed, and a wide range of statistical techniques are available for analyzing abundance estimates obtained using each of them (Krebs 1999; Williams et al. 2002).

A. Area-based counts In an *area-based count*, as its name suggests, the individuals in a given area or volume are counted. This method may make use of a *quadrat* (**Figure A**), which is a sampling area (or volume) of any size or shape, such as a 1 m^2 circular plot used to count small plants, a 0.1 ha plot used to count trees, or a soil core of a certain diameter and depth used to count soil organisms. The counts from several quadrats are then summed and averaged to estimate the number of individuals per unit of area (or volume).

Area-based counts are often used to estimate absolute population sizes of organisms that are sessile (e.g., plants) or can move only short distances during the time it takes to count the individuals in a quadrat (e.g., sea urchins). Area-based counts can also be used to estimate the abundances of more mobile organisms, as when large mammals are observed in aerial surveys. Area-based counts of highly mobile organisms can provide estimates of relative population sizes; further information (such as the probability that an organism will be present but not seen when surveyed by air) may be required before such counts can be used to estimate absolute population sizes.

Figure A An Underwater Quadrat A marine biologist counts the abundances of coral species found on a reef off the Caroline Islands, Micronesia.

B. Distance methods In *distance methods*, an observer measures the distances of individuals seen from a line or a point; these distances are then converted into estimates of the number of individuals per unit of area. For example, distance methods often use *line transects*, straight lines from which the distance to each individual is measured (**Figure B**). For organisms that move quickly or are hard to detect, the number of individuals observed along a line transect provides an estimate of relative population size.

For both mobile and sessile organisms, distances recorded along a transect can also be used to estimate the absolute abundance; this conversion can be made if it is possible to determine a *detection function*, which accounts for how the chance of seeing an individual decreases with its distance from the transect. Other distance methods include *point sampling* techniques, in which the distance to the nearest (visible) individual is measured from a series of locations or "points"; as with line transect data, a detection function is used to convert these distances into estimates of the absolute population size (see Krebs 1999; Schwarz and Seber 1999).

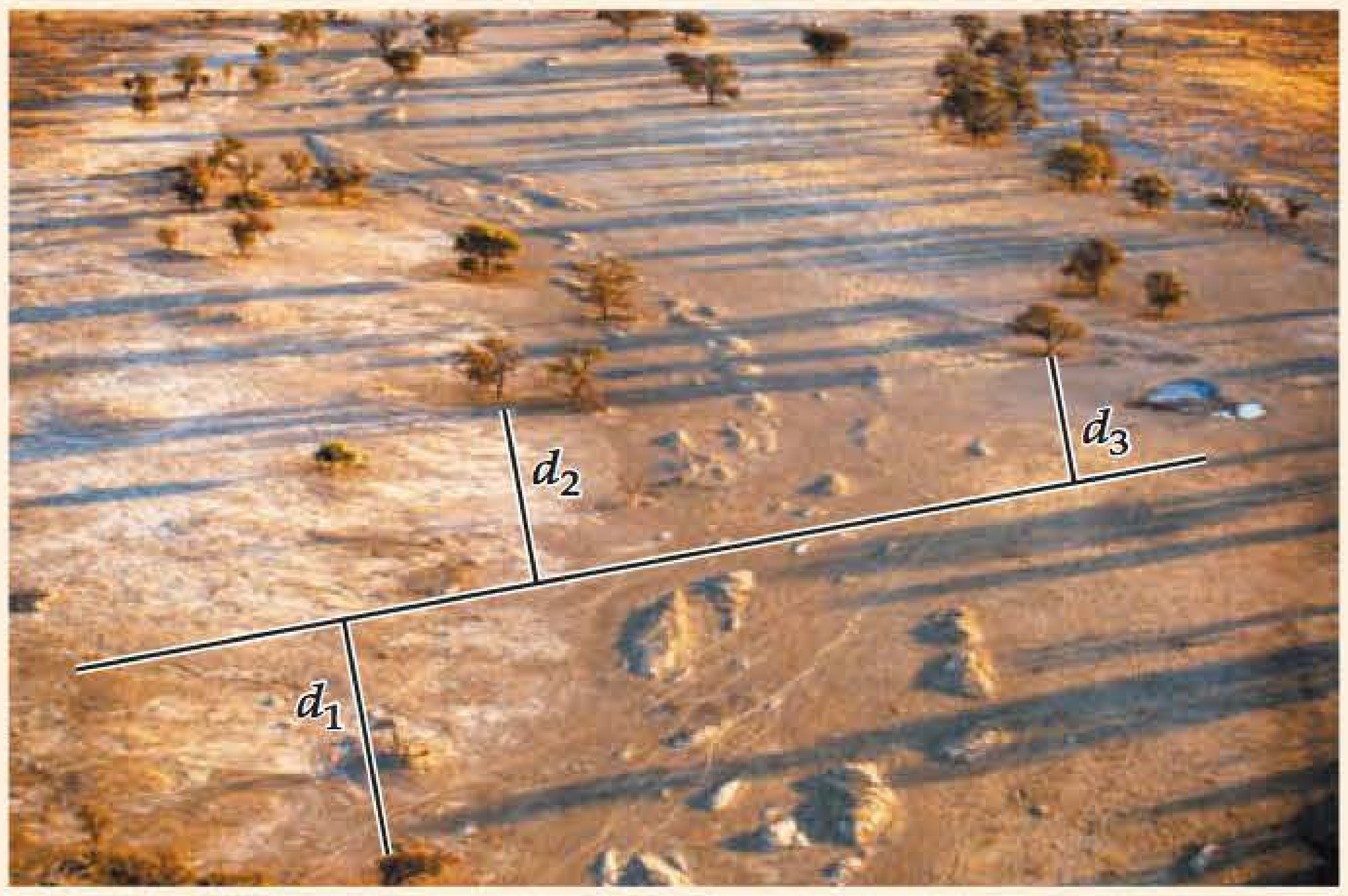


Figure B Counting Trees from a Line Transect The density of these camelthorn trees (*Acacia erioloba*) in Kgalagadi Transfrontier Park, South Africa, could be estimated using a line transect, as shown here.

Figure C Release of Marked Salmon To obtain mark–recapture estimates of salmon abundance, ecologists tag and then release marked salmon (note the two tags near the dorsal fin).

C. Mark–recapture studies In *mark–recapture studies*, a subset of the individuals in a population is captured, marked (as with a tag or dot of paint) so that they can be recognized at a later time, and released (**Figure C**). After the marked individuals have been given enough time to recover and move throughout the population, individuals are captured a second time, and the proportion of marked individuals found in the second capture is used to estimate the total population size.

Mark–recapture methods are used to estimate the absolute population size of mobile organisms; they are also used to obtain data on the survival or movement of individuals. The simplest mark–recapture method is summarized by Equation 9.3; use of this equation assumes that (1) the population size does not change during the sampling period (no births, deaths, immigration, or emigration), (2) each individual has an equal chance of being caught, (3) marking does not harm individuals or alter their behavior (such as by making them harder to recapture), and (4) marks are not lost over time. A wide range of other mark–recapture methods have been developed to address cases in which one or more of these assumptions are violated (Krebs 1999; Schwarz and Seber 1999; Williams et al. 2002).

original proportion we caught, M_1/N. Thus, we have the equation

$$M_1/N = R/M_2 \tag{9.2}$$

We can rearrange Equation 9.2 to estimate the total number of butterflies in the meadow as

$$N = (M_1 \times M_2)/R \tag{9.3}$$

which in this case would equal $(23 \times 15)/4 = 86$.

We'll close this section with two examples of how abundance and distribution data are collected and used, the first of which highlights how long-term ecological data sets can contribute to efforts to solve applied problems.

Ecologists used abundance data to track down a mysterious disease

In 1993, dozens of people in the Four Corners region of the southwestern United States became sick with flu-like symptoms and shortness of breath, and 60% of them died within a few days of becoming ill. No one had seen this combination of symptoms before. An outbreak of a lethal, previously unknown disease appeared to be in progress, and there was no cure or successful treatment.

The U.S. Centers for Disease Control (CDC) quickly identified the disease agent as a new strain of hantavirus carried by the deer mouse (*Peromyscus maniculatus*). Seeking more information about the new disease, now known as hantavirus pulmonary syndrome, or HPS, the CDC contacted ecologists who had been studying mouse populations in the Southwest. Examination of deer mouse specimens collected between 1979 and 1992 revealed that the virus had been present in the area for more than 10 years prior to the outbreak. Why, then, did the outbreak of HPS occur in 1993 and not before?

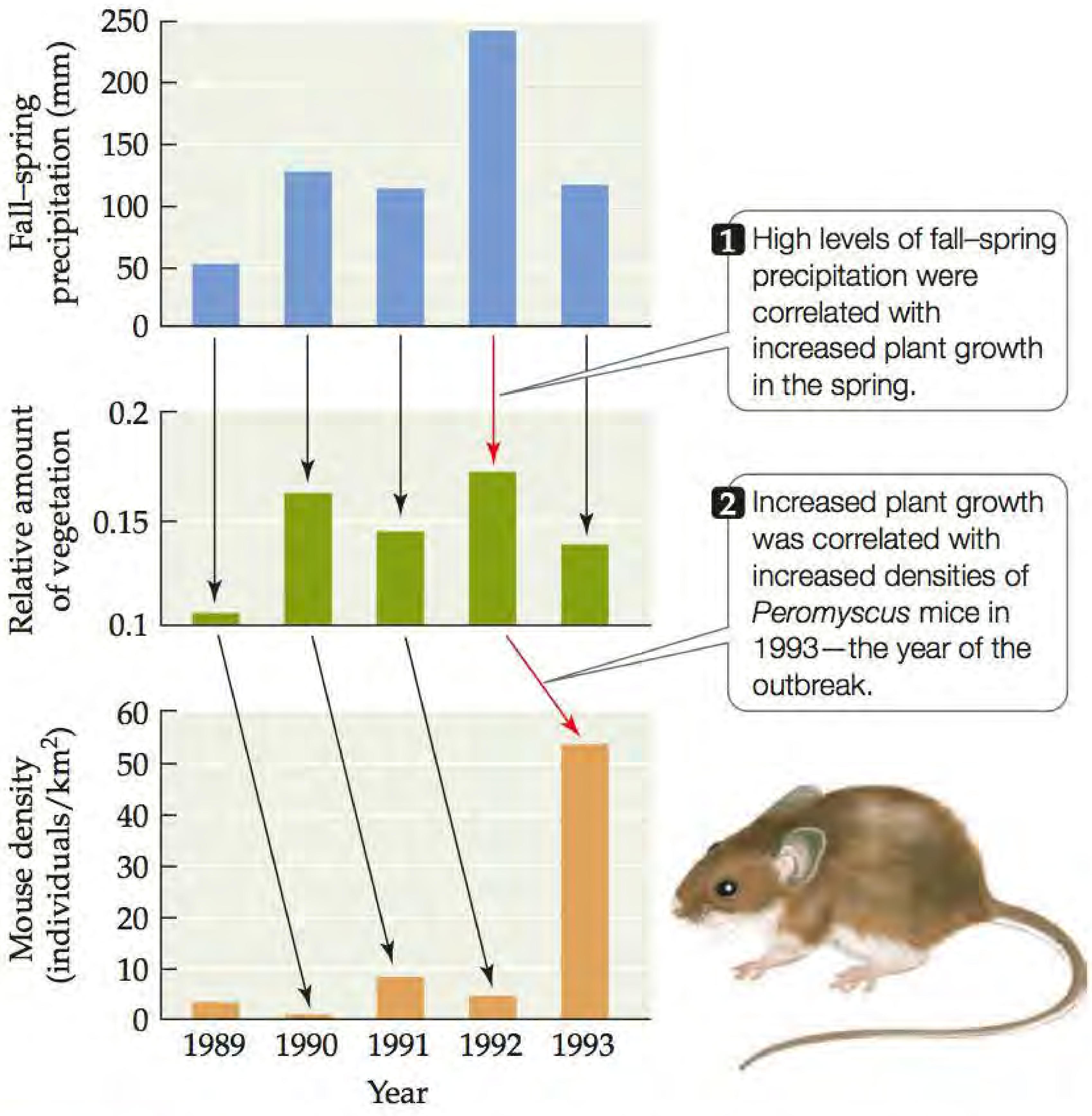
To address this question, ecologists used data on the abundances of *Peromyscus* species collected since 1989 at the nearby Sevilleta National Wildlife Refuge. These data showed that the densities of several *Peromyscus* species had increased 3–20-fold between 1992 and 1993. Next, a series of satellite images was used to develop an index of how much plant matter was available as food for *Peromyscus* at different times. When that index was compared with precipitation data, the results suggested that unusually high rainfall from September 1991 through May 1992 had led to enhanced plant growth in spring 1992 (**Figure 9.17**). In turn, the enhanced plant growth produced abundant food for rodents (seeds, berries, green plant matter, arthropods), which allowed mouse populations to increase in size by 1993—the year of the HPS outbreak.

Rodents shed hantavirus in their urine, feces, and saliva; hence, high mouse numbers, which led to increased mouse–human contact, were thought to be the cause of the 1993 outbreak. For *Peromyscus* to spread HPS to people, however, the mice must be infected with hantavirus. Disease outbreaks are most likely to occur when both mouse densities and mouse infection rates are high, but the factors that cause that outcome remain only partially understood. Moreover, it is clear that the actual risk to people varies greatly with location and depends on such factors as habitat type (which can influence mouse movements), microclimate (e.g., in arid regions, nearby areas often experience very different amounts of rainfall), and local food abundance. Overall, we now know enough about HPS to predict periods of heightened risk to human populations, but more remains to be learned before we can predict the specific locations most at risk.

How could we predict exactly where infected deer mice would be found? We turn next to a technique that has proved helpful in predicting the locations of other organisms: niche models.

Niche models can be used to predict where species can be found

To determine the geographic distribution of a species, scientists record all locations where the species is found. Most of our examples thus far in this chapter have involved species whose distributions are well understood. However, there are many species whose geographic ranges are not yet known. When such species are rare or in need of protection, it can be difficult to plan how best to protect them. Furthermore, ecologists often want



1 High levels of fall–spring precipitation were correlated with increased plant growth in the spring.

2 Increased plant growth was correlated with increased densities of *Peromyscus* mice in 1993—the year of the outbreak.

Figure 9.17 From Rain to Plants to Mice The outbreak of hantavirus pulmonary syndrome in the southwestern United States in 1993 may have been caused by a series of interconnected events. (After Yates et al. 2002.)

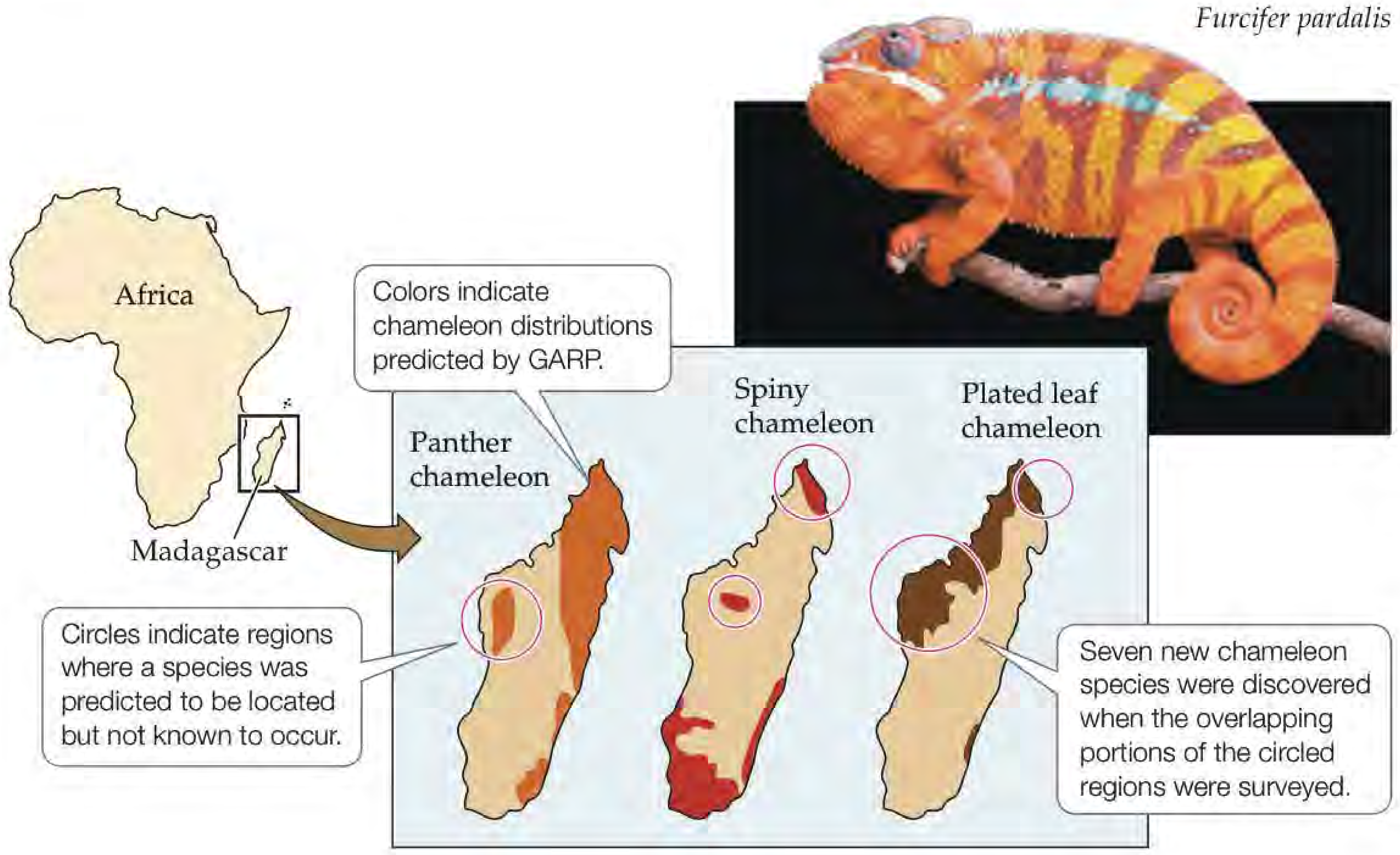
to predict *future* distributions of species—for example, whether and how a pest species will spread after it has been introduced to a new geographic region. Scientists and policymakers face similar challenges when they seek to predict how distributions of species will shift in response to global climate change.

One way to predict the current or future distribution of a species is to characterize its **ecological niche**, the abiotic and biotic conditions that the species needs to grow, survive, and reproduce. Such information can be used to construct a **niche model**, a tool that predicts a species' geographic distribution based on the environmental conditions at locations the species is known to occupy.

Investigators from the United States and Mexico used such an approach to predict the distributions of chameleons in Madagascar (Raxworthy et al. 2003). The researchers obtained information about vegetation cover (from satellite images), temperature, precipitation, topography (elevation, slope, aspect), and hydrology (water flow, tendency to pool) from government and commercial sources. Values for these environmental variables were recorded for each of a series of 1 × 1 km^2 areas (referred to as grid cells) that covered all of Madagascar. Next, for each of 11 chameleon species, rules were developed that described the environmental conditions in which the species was most likely to be found; we'll refer to these rules as habitat rules.

There are many different ways to develop such habitat rules. The chameleon study used a computer program that compared the environmental conditions of grid cells selected at random from a map of Madagascar with the environmental conditions of grid cells where a chameleon species was known to occur. The program then searched for accurate habitat rules using a flexible approach known as GARP (*G*enetic *A*lgorithm for *R*ule-Set *P*roduction). This search mechanism works by changing habitat rules in a way that mimics the occurrence of genetic mutations (random changes in the DNA sequence of an organism) and natural selection. For example, initially a habitat rule might state that a species should be found in regions where the temperature ranges from 15°C to 25°C and the elevation ranges from 300 to 550 m. This rule might "mutate" at random to a temperature range of 15°C–30°C and an elevation range of 300–500 m. If the new rule improves the ability of the program to predict where the species is actually found, it is retained, and other, less successful rules are discarded.

For the Madagascar chameleons, the accuracy of the niche model developed using GARP was tested with chameleon location data that had not been entered into the program. The model performed well, correctly predicting where these chameleons lived 75%–85% of the time. Next, the model was used to predict the geographic ranges of each of the 11 chameleon species—information that will be useful in efforts to protect chameleon habitat. Finally, the researchers investigated an interesting "error" in the model: there were several overlapping areas in which the model predicted that 2 or more of the 11 species would be found but in which no chameleons were known to occur (**Figure 9.18**). When two of these overlapping areas were surveyed, 7 previously unknown chameleon species were discovered. More intensive surveys conducted at the same time, but at sites outside these overlapping areas, found only 2 new species. Thus, the scientists were able to predict both the distributions of known chameleon species and the locations of habitats suitable for other chameleons, and the latter prediction led to the discovery of 7 new chameleon species.



Colors indicate chameleon distributions predicted by GARP.

Circles indicate regions where a species was predicted to be located but not known to occur.

Seven new chameleon species were discovered when the overlapping portions of the circled regions were surveyed.

Figure 9.18 Predicted Distributions of Madagascar Chameleons The distributions predicted by GARP are shown for the panther chameleon (*Furcifer pardalis*), the spiny chameleon (*F. verrucosus*), and the plated leaf chameleon (*Brookesia stumpffi*), 3 of the 11 Madagascar chameleon species studied by Raxworthy et al. All 11 of the predicted distributions proved accurate. (After Raxworthy et al. 2003.)

A CASE STUDY REVISITED

From Kelp Forest to Urchin Barren

When sea urchins graze kelp so heavily that kelp forests are replaced by urchin barrens, what happens next? We might expect that the urchins would starve because they have destroyed their food source. Field studies show that urchin barrens can persist for years on end, however, because urchins can use food sources other than kelp, including benthic diatoms, less preferred algae (including hard, encrusting forms that cover rock surfaces), and detritus. When food is extremely scarce, urchins can reduce their metabolic rate, reabsorb their sex organs (forgoing reproduction but increasing their chances of survival), and absorb dissolved nutrients directly from seawater.

As tough and resilient as urchins are, they are vulnerable to predation by sea otters (*Enhydra lutris*), which function as impressive urchin-eating machines. Otters need to eat large quantities of food each day because they have a high metabolic rate and they store little energy as fat. Urchins are a favorite food of otters, and since there are 20–30 otters per square kilometer around some Aleutian islands, the potential exists for otters to consume enormous quantities of urchins. These facts, coupled with the observation that urchins usually are common only where otters are absent, led investigators to suspect that otters might control the locations of urchins, and hence the locations of kelp forests.

To test this hypothesis, Estes and Duggins (1995) compared sites with and without otters, both in the Aleutian Islands and along the coast of southern Alaska. Confirming the results of previous studies, they found that sites where otters had been present for a long time usually had many kelp and few urchins, whereas sites without otters usually had many urchins and few kelp. Estes and Duggins also collected data from sites colonized by otters during the course of their study. At sites in southern Alaska, the arrival of otters had a rapid and dramatic effect: within 2 years, urchins virtually disappeared, and kelp densities increased dramatically (**Figure 9.19A**). At Aleutian Islands sites, however, kelp recovered more slowly after the arrival of otters (**Figure 9.19B**). At these sites, otters ate most of the large urchins, reducing urchin biomass by an average of 50%. However, in a twist that did not occur at the southern Alaska sites, the arrival of new urchin larvae (most likely via ocean currents) provided a steady supply of small urchins. These small urchins slowed the rate at which kelp forests replaced urchin barrens.

Historically, sea otters were abundant throughout the North Pacific, but by 1900 they had been hunted (for fur) to near extinction. By 1911, when international treaties protected the sea otter, only about 1,000 otters remained—less than 1% of their early numbers. Scattered colonies of otters survived and gradually increased in size around some Aleutian islands, causing the observed pattern of kelp forests around some islands, urchin barrens around others. In the 1990s, however, there was a sudden and unexpected decline in otter populations. Urchins made a

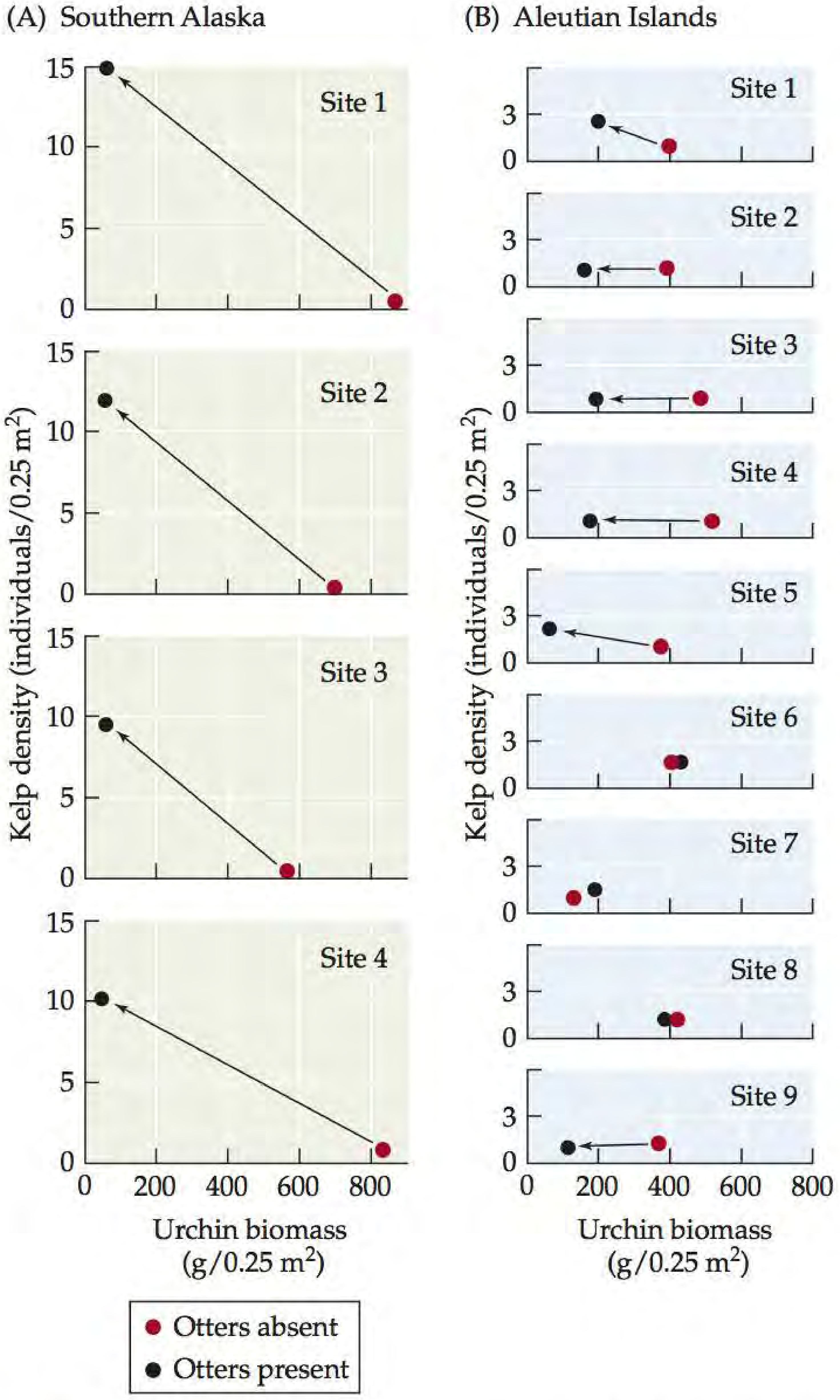


Figure 9.19 The Effect of Otters on Urchins and Kelp Plots of kelp density versus sea urchin biomass measured at sites in southern Alaska and in the Aleutian Islands before and 2 years after the return of otters. (A) Two years after otters colonized four sites in southern Alaska, urchin biomass had declined considerably, and kelp density had increased substantially at all sites. (B) Two years after otters colonized nine sites in the Aleutian Islands, sea urchin biomass had declined at six of the sites, but kelp showed clear signs of recovery at only two of the sites. Arrows indicate a decline in urchin biomass and (at some sites) an increase in kelp density in the presence of otters. (After Estes and Duggins 1995.)

? For the nine sites in (B), list the six sites where urchin biomass declined; also list the two sites where kelp density increased.

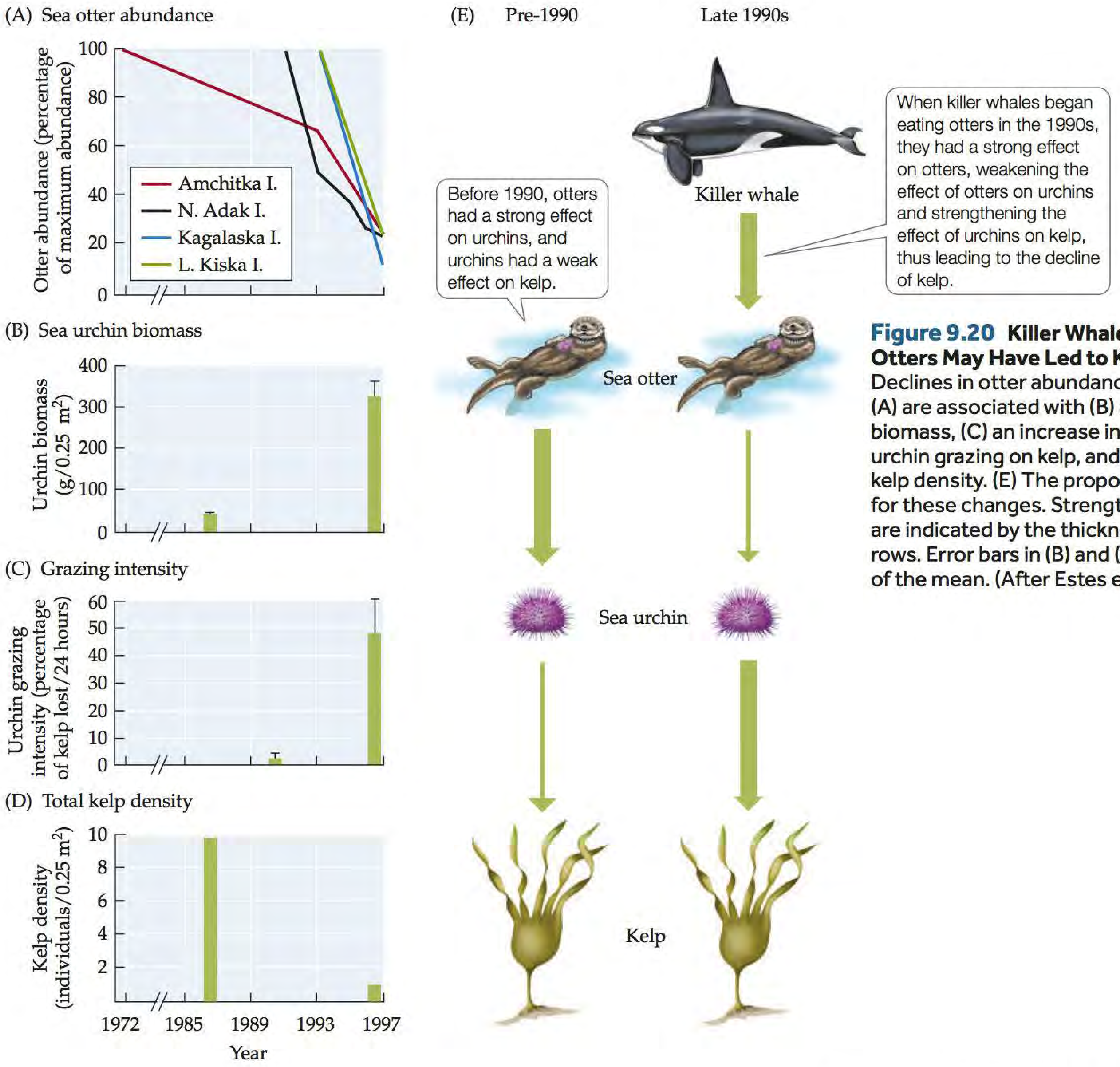


Figure 9.20 Killer Whale Predation on Otters May Have Led to Kelp Declines Declines in otter abundance over time (A) are associated with (B) a rise in urchin biomass, (C) an increase in the intensity of urchin grazing on kelp, and (D) a decrease in kelp density. (E) The proposed mechanisms for these changes. Strengths of the effects are indicated by the thicknesses of the arrows. Error bars in (B) and (C) show one SE of the mean. (After Estes et al. 1998.)

comeback, and kelp densities were reduced (**Figure 9.20A–D**). The question then became, What caused the decline of sea otter populations in the 1990s?

James Estes and his colleagues have suggested that otters declined because of increased predation by the killer whale, *Orcinus orca* (**Figure 9.20E**). It is not known why killer whales began to eat more otters. Some researchers have argued that this change may have been part of a chain of events that began when commercial whaling drove populations of large whales to low numbers (Springer et al. 2003). According to this hypothesis, once their preferred prey (large whales) became rare, killer whales began to hunt a series of other species (first harbor seals, then fur seals, then sea lions), each of which then also declined in number. Other researchers dispute the connection between commercial whaling and the decline of seals and sea lions, suggesting that seal and sea lion populations declined for other reasons, such as a lack of food due to reduced fish populations in the open ocean (DeMaster et al. 2006). Whatever the cause, it was in the 1990s, when populations of harbor seals, fur seals, and sea lions had all declined to low levels, that killer whales were first seen attacking otters. Otters and killer whales had been observed in close proximity for decades, but within 10 years of the first known attack, otter populations crashed.

CONNECTIONS IN NATURE
From Urchins to Ecosystems

Urchins, otters, and perhaps killer whales and people play important roles in determining the distribution of kelp. But does the presence or absence of kelp matter? Do kelp have strong effects on nearshore ecosystems?

Indeed they do. Kelp forests are among the most productive ecosystems in the world, rivaling tropical forests in the amount of new biomass they produce each year (up to 2,000 g of carbon/m^2/year). Kelp strands grow from their base, and their tips are constantly "eroded" by wave action and other physical forces. Thus, much of their biomass ends up as floating bits of detritus, which provides food for suspension feeders such as barnacles and mussels that filter food from the water. As a result, barnacles and mussels grow more rapidly and are more abundant in kelp forests than in urchin barrens. Carbon-13 labeling studies (see Ecological Toolkit 5.1) have shown that the sugars kelp produce by photosynthesis provide a food source for a wide range of species (Duggins et al. 1989). Kelp forests also serve as nurseries for the young of many marine species and as havens from predators for the adults of still more species.

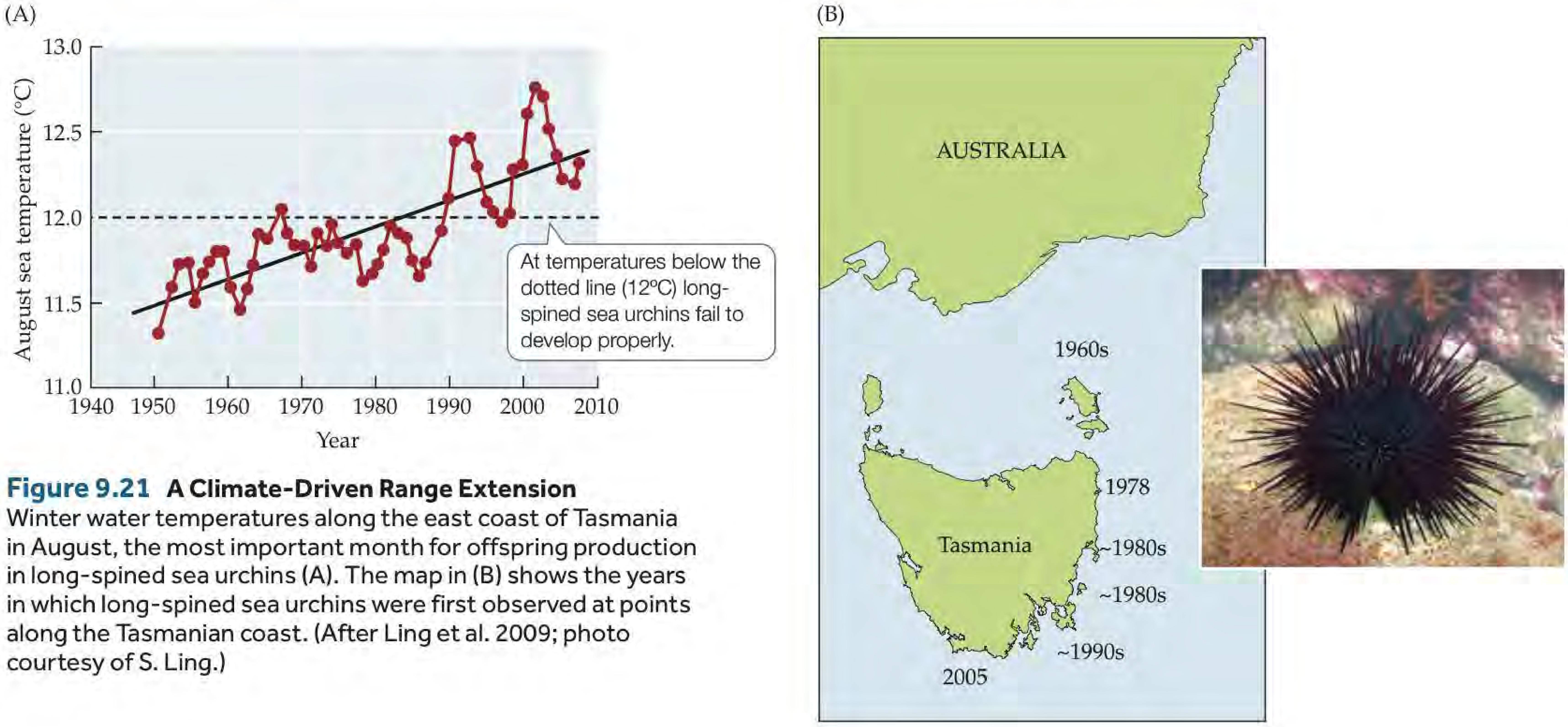
Overall, we can see that the effects of urchins on kelp, and of otters on urchins, do indeed matter: urchins and otters (and killer whales) set into motion a chain of events that alters fundamental aspects of the marine ecosystem. A similar chain of events seems to have affected kelp ecosystems along the coast of Tasmania, Australia. However, the events in Tasmania may be driven by an additional factor: climate change.

CLIMATE CHANGE CONNECTION

Effects of Climate Change on the Geographic Distributions of Species The waters along the east coast of Tasmania have warmed considerably since 1950 (**Figure 9.21A**). As this warming has occurred, the long-spined sea urchin (*Centrostephanus rodgersii*) has extended its range to the south (**Figure 9.21B**). The changes in the distribution of this urchin are consistent with the idea that climate change is the underlying cause: the larvae of *C. rodgersii* fail to develop properly in waters colder than 12°C, and the urchin has moved into new regions as waters in those locations have warmed to the point that they remain above that temperature. As *C. rodgersii* has expanded its range, it has established extensive urchin barrens in which all kelp have been removed by grazing (Ling 2008). Thus, through its effects on the geographic distribution of the long-spined sea urchin, ongoing climate change appears to be having a profound effect on kelp ecosystems along the Tasmanian coast. (For more information about how this example connects to other levels of the ecological hierarchy, see **Online Climate Change Connection 9.1**.)

As observed for the long-spined sea urchin, shifts in the geographic distributions of hundreds of other species have been linked to climate change (Parmesan and Yohe 2003). In some marine communities, range shifts driven by climate change have contributed to the rapid replacement of temperate species with species from subtropical or tropical regions, leading to the formation of entirely new communities (Wernberg et al. 2016). On land, many species in the Northern Hemisphere have expanded the northern edges of their ranges toward the pole, while the southern edges of their ranges have maintained relatively stable positions (Sunday et al. 2012). But range shifts do not always occur in this way, nor do they necessarily keep pace with ongoing climate change.

For example, Kerr et al. (2015) found that the geographic ranges of 67 species of bumblebees have shown



At temperatures below the dotted line (12ºC) long-spined sea urchins fail to develop properly.

Figure 9.21 A Climate-Driven Range Extension Winter water temperatures along the east coast of Tasmania in August, the most important month for offspring production in long-spined sea urchins (A). The map in (B) shows the years in which long-spined sea urchins were first observed at points along the Tasmanian coast. (After Ling et al. 2009; photo courtesy of S. Ling.)

rapid losses in the south and only a slow expansion in the north—as a result, their ranges are shrinking and the populations of some bumblebee species have declined as the climate has warmed. Moreover, even when the range expansion of one or more species keeps pace with climate change, such range shifts can have cascading and wide-ranging effects on other species (as illustrated by the decimation of kelp forests as the long-spined sea urchin expanded its range to the south). The exact nature of such cascading effects can be hard to predict, but it is clear that ongoing climate change will have major effects on ecosystems throughout the globe.

Summary

CONCEPT 9.1 Populations are dynamic entities that vary in size over time and space.

- Populations are groups of individuals of a species that live in the same area and interact with one another.
- The number of individuals in a population changes over time and from one place to another.
- Dispersal can link the populations of a species to one another.
- In species that can reproduce asexually, the members of a population can be defined in terms of genetic individuals (genets) or physiological individuals (ramets).

CONCEPT 9.2 The distributions and abundances of organisms are limited by habitat suitability, historical factors, and dispersal.

- The presence of suitable habitat limits the distributions and abundances of organisms.
- The suitability of habitat depends on abiotic and biotic features of the environment, the interaction between abiotic and biotic factors, and disturbance.
- Dispersal and events in the evolutionary and geologic history of Earth also influence the distribution and abundance of organisms.

CONCEPT 9.3 Many species have a patchy distribution of populations across their geographic range.

- No species is found everywhere because much of Earth is not suitable habitat for its populations.
- Geographic ranges vary considerably in size from one species to another.
- Many populations have a patchy distribution at both small and large spatial scales.

CONCEPT 9.4 The dispersion of individuals within a population depends on the location of essential resources, competition, dispersal, and behavioral interactions.

- The dispersion of individuals within a population may be regular, random, or clumped. In the field, clumped dispersions are most common.
- A random or clumped dispersion may match the spatial arrangement of favorable environmental conditions. Clumping may also result from short dispersal distances. Competition can produce a nearly regular dispersion.
- Behavioral interactions in which individuals repel or attract one another can affect the dispersion of individuals within a population.

CONCEPT 9.5 Population abundances and distributions can be estimated with area-based counts, distance methods, mark–recapture studies, and niche models.

- The most direct way to determine the number of individuals in a population is to count all of them. When this is not possible or practical, area-based counts, distance methods, or mark–recapture studies can be used to estimate the number of individuals in a population.
- The geographic distribution of a species can be analyzed in terms of its ecological niche, the abiotic and biotic conditions of the environment that the organisms need to grow, survive, and reproduce.
- Niche models can be used to estimate the distribution of a species when we have insufficient data on its geographic range or when we want to predict the future locations of its populations.

Review Questions

1. Describe some of the complicating factors that can be encountered in studying a population.
2. No species is found everywhere on Earth. Why? Your answer should include an explanation of why organisms are not found in all places where you might expect them to thrive.
3. What is a niche model? Describe how such a model could be used to predict the future distribution of an organism that is spreading into a new geographic region.
4. Sea otters can eat 20%–23% of their body weight in food each day. An average sea otter weighs 23 kg (roughly 50 pounds), and there are 20–30 otters per square kilometer where they are present. An average sea urchin weighs 0.55 kg. Assuming that the otters eat only sea urchins, use these data to calculate a conservative estimate of the number of sea urchins per square kilometer that an otter population would be expected to eat each year.

Hone Your Problem-Solving Skills

Climate warming has enabled the long-spined sea urchin (*Centrostephanus rodgersii*) to expand its range poleward along the east coast of Tasmania, Australia (see Figure 9.21). To assess the impact of this range shift, Scott Ling (2008), then a graduate student at University of Tasmania, estimated the number of taxa and total number of individuals in areas where (1) urchins had yet to colonize ("intact kelp beds"), (2) urchins were experimentally removed ("recovered kelp beds"), and (3) urchins had colonized and were not removed ("urchins present"). For each treatment, he placed four 0.25 m^2 quadrats on each of three patches. Data are shown in the table.

1. What is the total number of quadrats from which data were collected in each patch? In each treatment? Use this information to calculate mean values for the total number of taxa and the total number of individuals in each of the three treatments.
2. Suppose that a patch from which urchins had been removed (a recovered kelp bed) and a patch in which urchins were present each had an area of 40 m^2. Use results from Question 1 to estimate the total number of individuals present in these two patches.
3. Interpret the results shown in the table.

TREATMENT	PATCH	TOTAL NO. OF TAXA (IN EACH OF 4 QUADRATS)	TOTAL NO. OF INDIVIDUALS (IN EACH OF 4 QUADRATS)
Intact kelp beds	1	61; 66; 44; 50	459; 402; 96; 179
	2	71; 87; 77; 66	497; 759; 560; 392
	3	69; 57; 90; 79	458; 188; 690; 533
Recovered kelp beds	1	84; 57; 79; 69	781; 341; 515; 771
	2	80; 86; 74; 61	401; 730; 429; 312
	3	72; 91; 69; 64	650; 1,132; 488; 419
Urchins present	1	11; 6; 9; 14	68; 36; 71; 47
	2	11; 22; 10; 15	38; 97; 33; 169
	3	12; 17; 13; 5	31; 134; 24; 14

ON THE COMPANION WEBSITE
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The website includes companions to all of the Analyzing Data exercises, Online Quizzes, Flashcards, Suggested Readings, and more. In addition, the following resources are available for this chapter:

Hands-On Problem Solving

9.1 Counting Beans: Effort and Accuracy of Population Estimates

9.2 Taking Over the World: Correlates of Cosmopolitan Distributions

Web Extensions

9.1 An Experimental Study on Dispersal and Abundance in Desert Pupfish

Online Climate Change Connection

9.1 Joint Effects of Climate Change and Overfishing

10 Population Growth and Regulation

KEY CONCEPTS

CONCEPT 10.1 Life tables show how survival and reproductive rates vary with age, size, or life cycle stage.

CONCEPT 10.2 Life table data can be used to project the future age structure, size, and growth rate of a population.

CONCEPT 10.3 Populations can grow exponentially when conditions are favorable, but exponential growth cannot continue indefinitely.

CONCEPT 10.4 Population size can be determined by density-dependent and density-independent factors.

CONCEPT 10.5 The logistic equation incorporates limits to growth and shows how a population may stabilize at a maximum size, the carrying capacity.

Human Population Growth: A Case Study

Viewed from space, Earth appears as a beautiful ball of blue and white in a vast sea of black. If we use satellite images to explore the surface of this beautiful ball in more detail, we find clear signs of human impacts across the globe. These signs range from the clear-cutting of tropical forests, to rivers that once meandered but now flow straight in channels dug by people, to surrealistic patterns formed by agricultural fields (**Figure 10.1**).

People have a large effect on the global environment for two underlying reasons: our population has grown explosively, and so has our use of energy and resources. The human population crossed the 7.3 billion mark in 2016, more than double the 3 billion people alive in 1960 (**Figure 10.2**). Our use of energy and resources has grown even more rapidly. From 1860 to 1991, for example, the human population quadrupled in size, but our energy consumption increased 93-fold.

The addition of more than 4 billion people since 1960 is remarkable. For thousands of years, the size of our population increased relatively slowly, reaching 1 billion for the first time in 1825 (Cohen 1995). The time we took to reach the 1 billion mark puts the current growth of our population in perspective: it took roughly 200,000 years (from the origin of our species to 1825) for the human population to reach its first billion, but now we are adding 1 billion people every 13 years. When did we switch from relatively slow to explosive increases in the size of our population?

No one knows for sure, since it is difficult to estimate population sizes from long ago. According to the best information we have, by 1550 there were roughly 500 million people alive, and the population was doubling every 275 years. By the time we reached our first billion in 1825, the human population was growing at a very rapid rate: it doubled from 1 to 2 billion by 1930, in just 105 years. Forty-five years later, it had doubled again, reaching 4 billion in 1975, at which time it was growing at an annual rate of nearly 2%. To appreciate what that means, a population with a 2% annual growth rate doubles in size every 35 years. If that rate of growth could be sustained, our population would double from 7.3 billion in 2016 to 14.6 billion in 2051, and would reach 26 billion by 2080.

What do you think the world would be like with 26 billion people? Already, with 7.3 billion people, we have transformed the planet. However, it is unlikely that there will be 26 billion people on Earth in 2080. Over the last 50 years, the rate of human population growth

Figure 10.1 **Transforming the Planet** This satellite image of a region in Bolivia shows how human actions have transformed tropical rain forests. Healthy vegetation is bright red in color. Loggers have cut long paths through what was once a vast, healthy forest, while ranchers have cleared large blocks of land for their herds. In several human settlements, a series of farms and fields radiate outward from a central point (where the settlement began). Only scattered parcels of healthy forest remain.

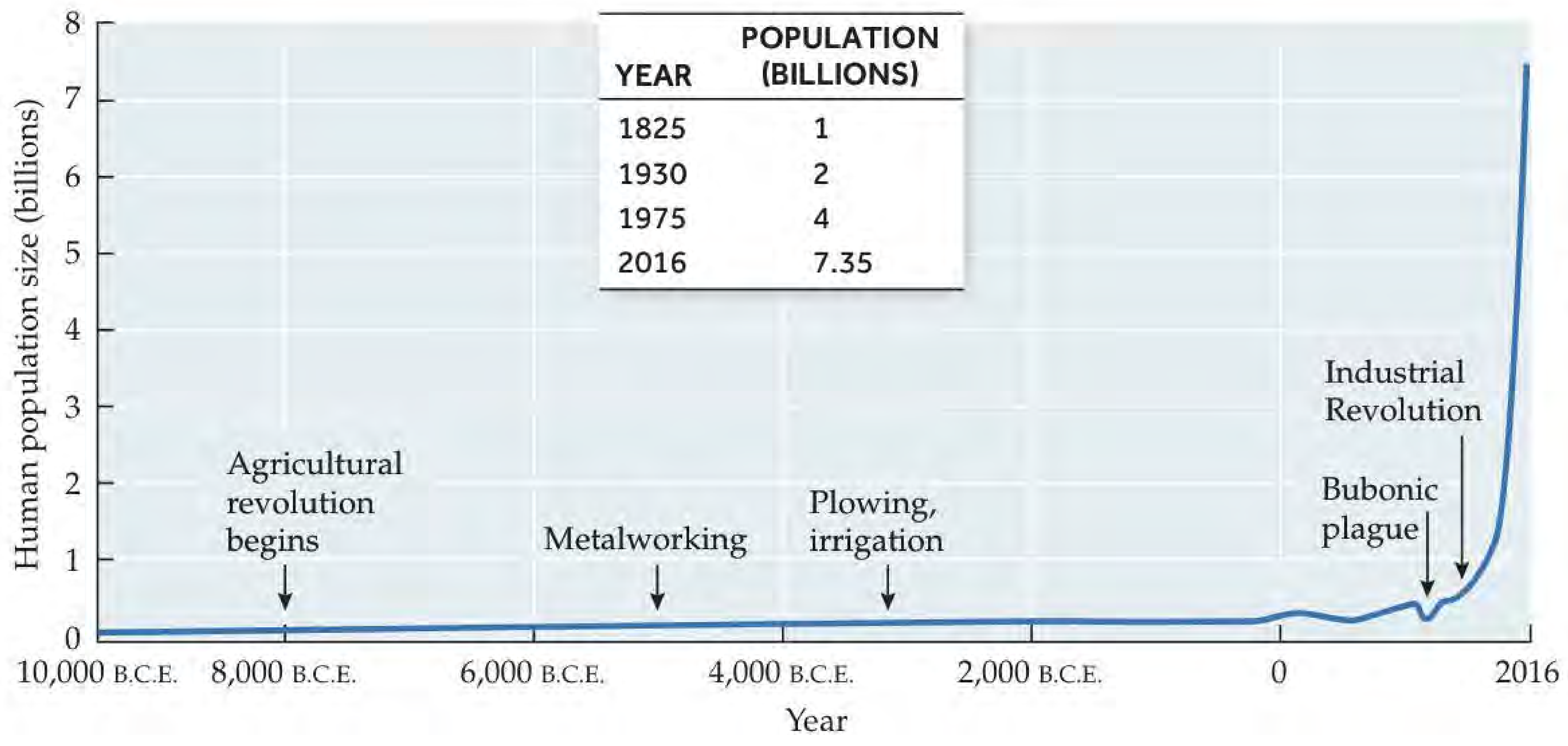


Figure 10.2 Explosive Growth of the Human Population The size of the human population increased relatively slowly until 1825, when the effects of the Industrial Revolution took hold. Since that time our population has increased in size by more than 6 billion people.

has slowed considerably, from a high of 2.2% per year in the early 1960s to the present rate of 1.1% annually. Even so, the current rate translates into a human population that is increasing by about 80 million people per year, more than 9,000 people each hour. Five countries—India, China, Pakistan, Nigeria, and the United States—account for almost half of this annual increase.

If the current annual growth rate of 1.1% were maintained, there would be more than 14 billion people on Earth in 2080. Can Earth support 14 billion people? Will there be that many people in 2080? Or will annual growth rates continue to fall? We'll return to these questions in the Case Study Revisited.

Introduction

One of the ecological maxims introduced in Table 1.1 reads, "No population can increase in size forever." Earth is a finite planet and hence cannot support ever-increasing numbers of any species. The limits imposed by a finite planet restrict what otherwise appears to be a universal feature of all species: a capacity for rapid population growth. As we saw in this chapter's Case Study, the human population is increasing rapidly. Other organisms, such as fungi known as giant puffballs, have an even more impressive capacity to increase their numbers. One of these fungi produces so many offspring per individual (7 *trillion*) that if all of them reached adulthood, the descendants of two individuals would weigh more than the entire planet in just two generations. But Earth is not covered with giant puffballs, or even people. The challenge for ecologists—whether they are studying giant puffballs, people, or any other organism—is to understand what factors promote population growth and what factors limit population growth.

What we learn can surprise us. We may find, for example, that current methods of protecting an endangered species work poorly. Such was the case for loggerhead sea turtles, a rare species whose young often die as they crawl to the sea after hatching from nests dug in the sand (**Figure 10.3**). Efforts to protect loggerheads initially focused on protecting newborns. However, researchers found that even if newborn survival could be increased to 100%, loggerhead populations would continue to decline. Fortunately, the researchers were able to use methods described

Figure 10.3 Dash to the Sea These loggerhead sea turtle hatchlings have emerged from nests in the sand and must reach the sea to survive. On land, eggs and hatchlings face threats from predators, beach development, and artificial lighting (which can disrupt the hatchlings' sense of direction, preventing them from reaching the sea). Loggerheads also face threats in the marine environment from predators, commercial fisheries (turtles can be caught accidentally in nets and traps), collisions with boats, and pollution.

in this chapter to identify more effective ways to protect loggerheads (see Ecological Toolkit 10.1).

How do scientists reach such conclusions? What data are needed? As we seek to understand population growth and its limits, some of the most powerful tools at our disposal are based on life tables, the topic we explore next.

CONCEPT 10.1

Life tables show how survival and reproductive rates vary with age, size, or life cycle stage.

Life Tables

Information about patterns of births and deaths in a population is essential if we want to understand current population trends or predict future population sizes. To obtain such information for a plant, for example, we could mark (e.g., with a numbered tag) a large number of individual seedlings shortly after they germinated. We could then follow the fate of each seedling over the course of one or more growing seasons. By recording whether each seedling was alive or dead at various points in time, we could estimate how the chance of surviving from one time period to the next varied with plant age. Similarly, by recording how many seeds each plant produced at different times, we could estimate how reproduction varied with age.

Life tables can be based on age, size, or life cycle stage

Scientists have collected data on patterns of births and deaths for plants, people, sea turtles, and many other organisms, and they have used these data to construct life tables. A **life table** provides a summary of how survival and reproductive rates vary with the age of the organisms. For example, **Table 10.1** shows data collected for the grass *Poa annua*. These data were collected by marking 843 naturally germinating seedlings and then following their fates over time. The column labeled Number alive, N_x, shows the number of individuals alive at age x, where x was measured in 3-month periods. As individuals die over time, N_x decreases steadily from the original 843 individuals, reaching 0 at $x = 8$ (24 months).

The next two columns in Table 10.1, S_x and l_x, are calculated from the N_x data. S_x is the age-specific **survival rate**, which is the chance that an individual of age x will survive to be age $x + 1$. S_2, for example, equals 0.6, which indicates that, on average, an individual of age $x = 2$ (6 months) has a 60% chance of surviving to reach age $x = 3$ (9 months). The next column, l_x, represents **survivorship**, which is the proportion of individuals that survive from birth (age 0) to age x. For example, l_3 equals 0.375, indicating that 37.5% of newborns survive to reach age $x = 3$. The final column, F_x, represents **fecundity**, which is the average number of offspring produced by a female while she is of age x.

Table 10.1 is an example of a **cohort life table**, in which the fate of a group of individuals born during the same time period (a *cohort*) is followed from birth to death. Cohort life tables are often used for plants or other sessile organisms because individuals can be marked and followed over time relatively easily. However, for organisms that are highly mobile or have long life spans (e.g., trees that live much longer than people), it is hard to observe the fate of individuals from birth to death. In some of these cases, a **static life table** can be used, in which the survival and reproduction of individuals of different ages during a single time period are recorded. To construct a static life table, one must be able to estimate the ages of the organisms under observation. Estimating ages is difficult in some species, but for others, reliable indicators of age are known, including annual growth rings in fish scales and tree wood and tooth wear in deer. Once ages have been estimated, age-specific birth rates can be determined by counting how many offspring the individuals of different ages produce. Age-specific survival rates can also be determined from a static life table (see Review Question 1), but only if we assume that survival rates have remained constant during the entire time that the individuals in the population have been alive—an assumption that may not be correct.

In discussing life tables, we have emphasized the importance of age because in many species, birth and death rates differ greatly among individuals of different ages. For other kinds of organisms, age is less important. In many plant species, for example, if conditions are favorable, a seedling may grow to full size relatively rapidly and reproduce at a young age. If conditions are not favorable, however, the plant may remain small for years and

TABLE 10.1 Life Table for the Grass *Poa annua*

AGE (IN 3 MO PERIODS), x	NUMBER ALIVE, N_x	SURVIVAL RATE, S_x	SURVIVORSHIP, l_x	FECUNDITY, F_x
0	843	0.856	1.000	0
1	722	0.730	0.856	300
2	527	0.600	0.625	620
3	316	0.456	0.375	430
4	144	0.375	0.171	210
5	54	0.278	0.064	60
6	15	0.200	0.018	30
7	3	0.000	0.004	10
8	0	—	0.000	—

Source: Data from Table 1.1 in Begon et al. (1996).

Note: Age (x) is measured in 3-month periods, so an individual of age $x = 5$, for example, is 15 months old.

N_x = number of individuals alive at age x.

S_x = proportion of individuals of age x that survive to age $x + 1$; $S_x = N_{x+1}/N_x$.

l_x = proportion of individuals that survive from birth (age 0) to age x; $l_x = N_x/N_0$.

F_x = average number of offspring born to a female while she is of age x.

reproduce little or not at all; if conditions become favorable at a later time, the plant may then grow to full size and reproduce. For such species, whether an individual reproduces or not is more closely related to size than to age. When birth and death rates correlate poorly with age, or when age is difficult to measure, life tables based on the sizes or the life cycle stages (e.g., newborn, juvenile, adult) of individuals in the population can be constructed.

Extensive life table data exist for people

Many economic, sociological, and medical applications rely on human life table data. Life insurance companies, for example, use census data to construct static life tables that provide a snapshot of current survival rates; they use these data to determine the premiums they charge customers of different ages. Let's consider two examples of human life tables, one from the United States, the other from Gambia.

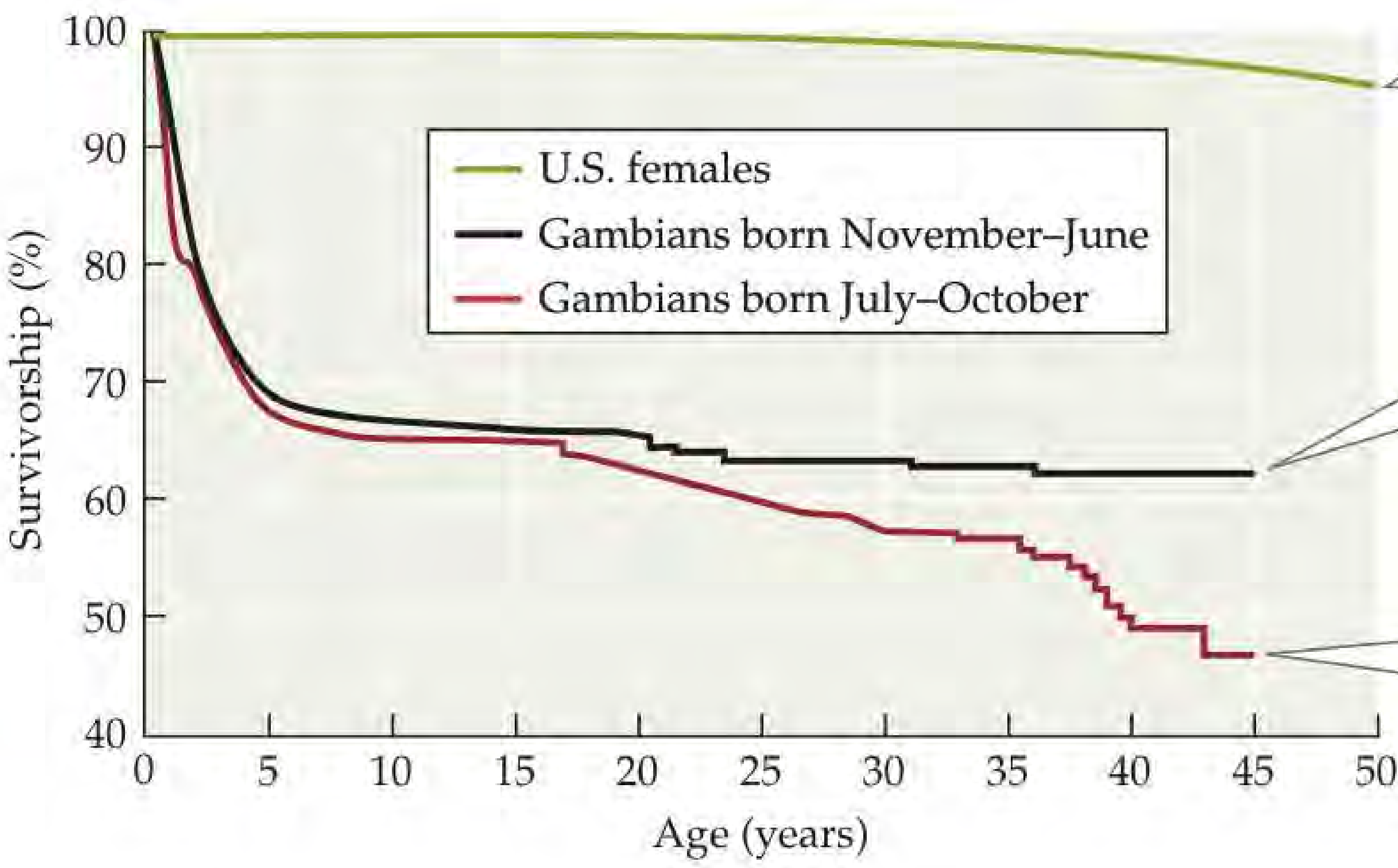
The U.S. Centers for Disease Control and Prevention periodically release reports that provide life table data for people in the United States. Reports released in 2009 and 2015 provide information on the survivorship (l_x), fecundity (F_x), and life expectancy (expected number of years of life remaining) of U.S. females of different ages (**Table 10.2**). To make their interpretation easier, such data can be graphed, as in **Figure 10.4**, which plots l_x data for U.S. females. This curve shows that survival probabilities for U.S. females remain high for many years; in fact, as Table 10.2 reveals, these survival probabilities do not begin to drop sharply until around age 70.

The data from the United States are in stark contrast to data from Gambia, a country located on the west coast of Africa. Moore et al. (1997) analyzed birth and death records for 3,102 people born in three Gambian villages between 1949 and 1994. They found that the season of birth had long-term effects: individuals born during the "hungry season" (July–October, when food stored from the previous year is in low supply) had lower survivorship as adults than did individuals born at other times of the year (see Figure 10.4). Their data also reveal large differences between the survivorship of people in Gambia and in the United States. For example, only 47%–62% of Gambians (depending on their season of birth) survived to reach age 45, whereas 97% of U.S. females survived to that age.

TABLE 10.2 Survivorship, Fecundity, and Years of Life Remaining by Age for U.S. Females

AGE (YR), x	SURVIVORSHIP, l_x	FECUNDITY, F_x	EXPECTED NO. OF YEARS OF LIFE REMAINING (AT AGE x)
0	1.0	0.0	81.8
1	0.994	0.0	80.5
5	0.994	0.0	76.6
10	0.993	0.0	71.6
15	0.992	0.004	66.7
20	0.991	0.203	61.7
25	0.989	0.511	56.9
30	0.986	0.578	52.0
35	0.982	0.479	47.2
40	0.977	0.232	42.4
45	0.970	0.046	37.8
50	0.958	0.003	33.2
55	0.940	0.0	28.8
60	0.915	0.0	24.5
65	0.880	0.0	20.3
70	0.828	0.0	16.5
75	0.752	0.0	12.9
80	0.640	0.0	9.6
85	0.485	0.0	6.9
90	0.292	0.0	4.8
95	0.119	0.0	3.3
100	0.027	0.0	2.3

Sources: Martin et al. 2009; Arias 2015.



The survivorship of U.S. females does not drop below 95% until after they are 50 years old.

Gambians born between November and June live longer …

… than Gambians born during the "hungry season."

Figure 10.4 Survivorship Varies among Human Populations In the United States, survivorship (l_x) does not drop greatly until old age. In Gambia, many people die at much younger ages. (U.S. data from Arias 2015; Gambia data from Moore et al. 1997.)

? The proportion of Gambians born in the hungry season who live to age 45 is roughly the same as the proportion of U.S. females who live to what age (see Table 10.2)?

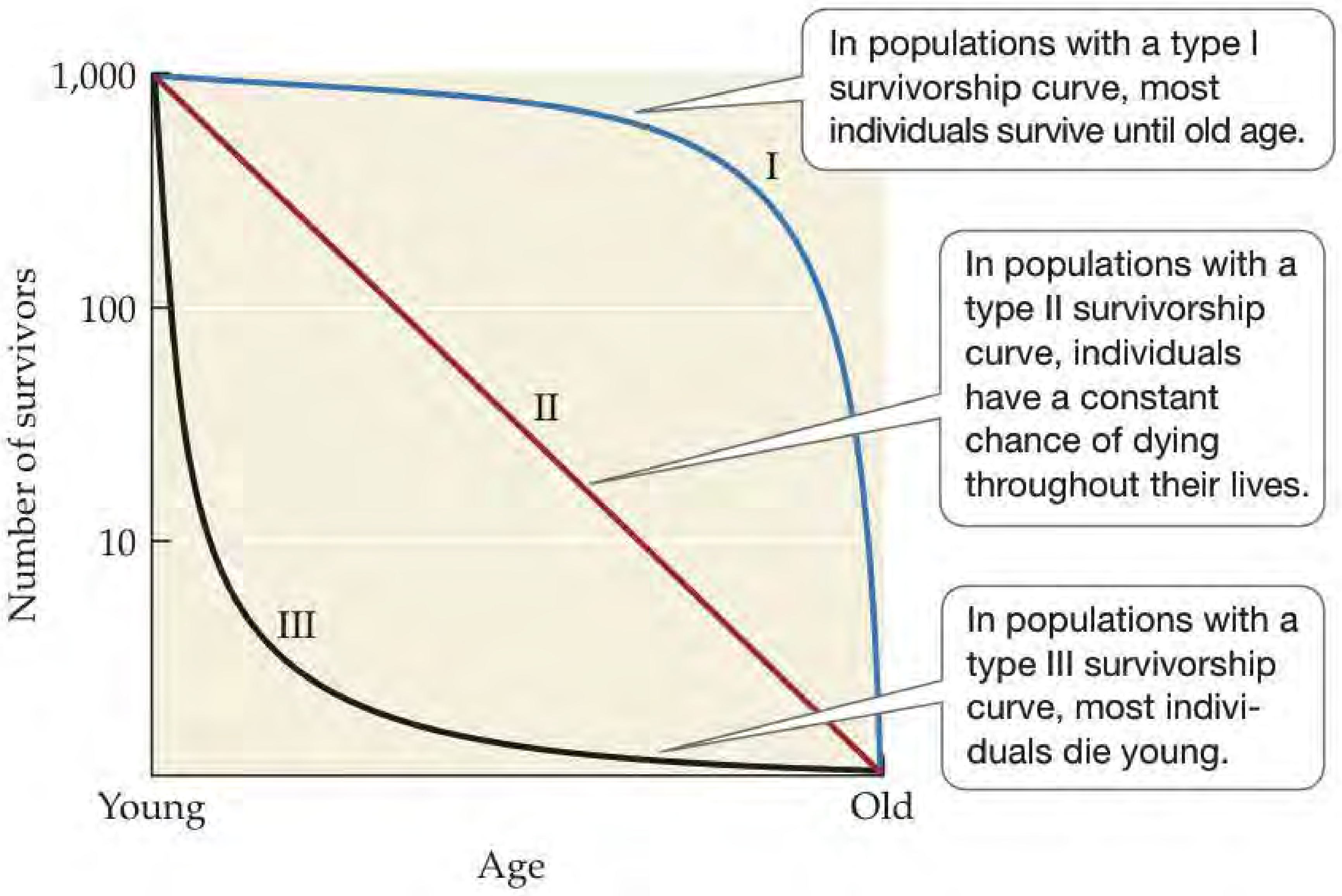


Figure 10.5 **Three Types of Survivorship Curves** The *y* axis of a survivorship curve is usually plotted on a logarithmic scale, as has been done here.

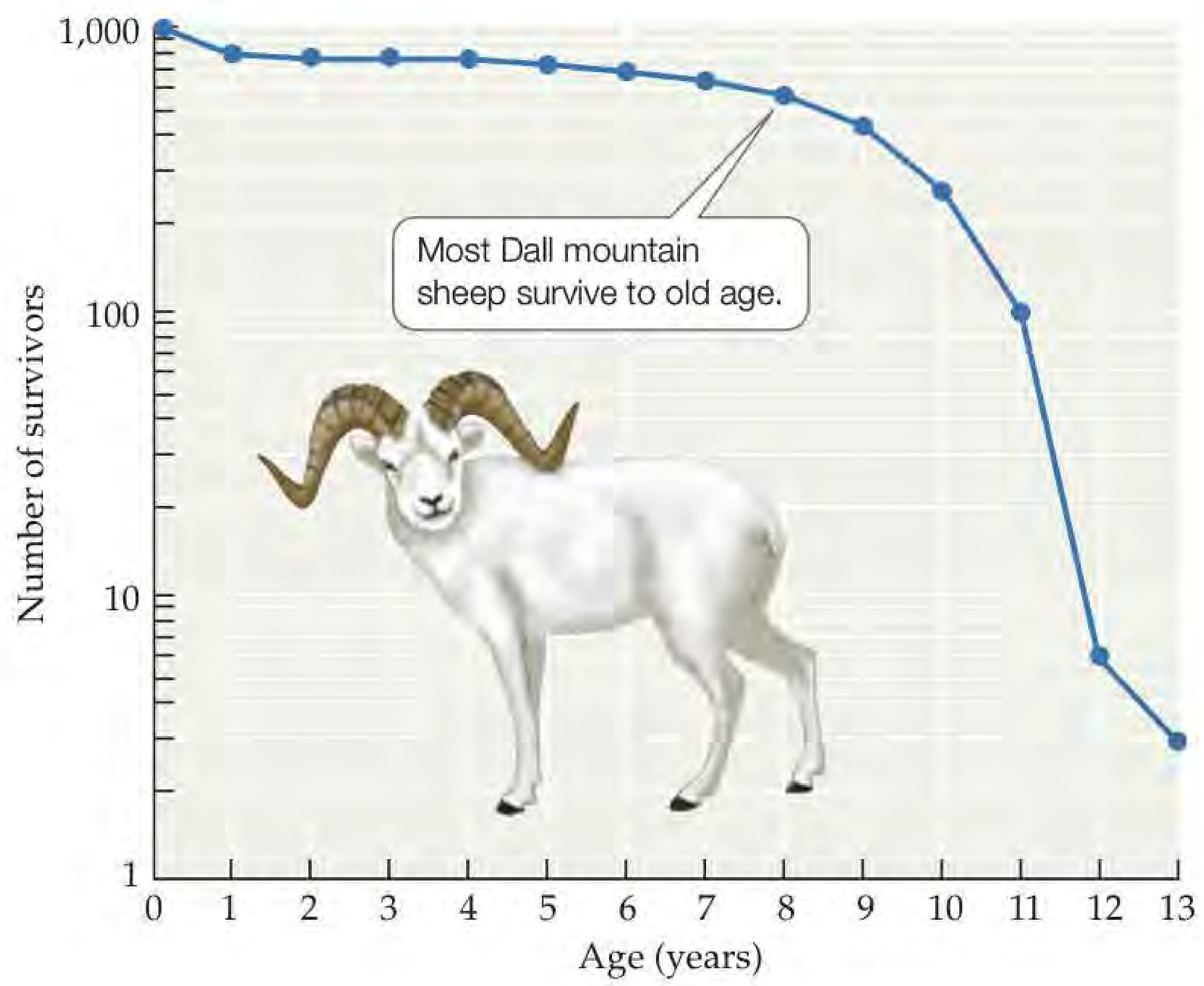
There are three types of survivorship curves

Survivorship data from life tables can be graphed as a **survivorship curve**. In such a curve, survivorship (l_x) data are used to plot the numbers of individuals from a hypothetical cohort (typically, of 1,000 individuals) that will survive to reach different ages. Results from studies on a variety of species suggest that survivorship curves can be classified into three general types, which indicate the life stages at which high rates of mortality are most likely to occur (**Figure 10.5**). In populations with a **type I survivorship curve**, newborns, juveniles, and young adults all have high survival rates; death rates do not begin to increase greatly until old age. Examples of populations with type I survivorship curves include U.S. females (see Figure 10.4) and Dall mountain sheep (**Figure 10.6A**). In populations with a **type II survivorship curve**, individuals have an approximately constant chance of surviving from one age to the next throughout their lives. Some bird species have a type II survivorship curve (**Figure 10.6B**), as do mud turtles (after their second year), some fishes, and some plant species. Finally, in populations with a **type III survivorship curve**, individuals die at very high rates when they are young, but those that reach adulthood survive well later in life. Type III survivorship curves—the most common type observed in nature—are typical of species that produce large numbers of young. Examples include

Figure 10.6 **Species with Type I, II, and III Survivorship Curves** Survivorship curves in (A) the Dall mountain sheep, (B) the song thrush, and (C) the desert shrub *Cleome droserifolia*. (A,B after Deevey 1947; C after Hegazy 1990.)

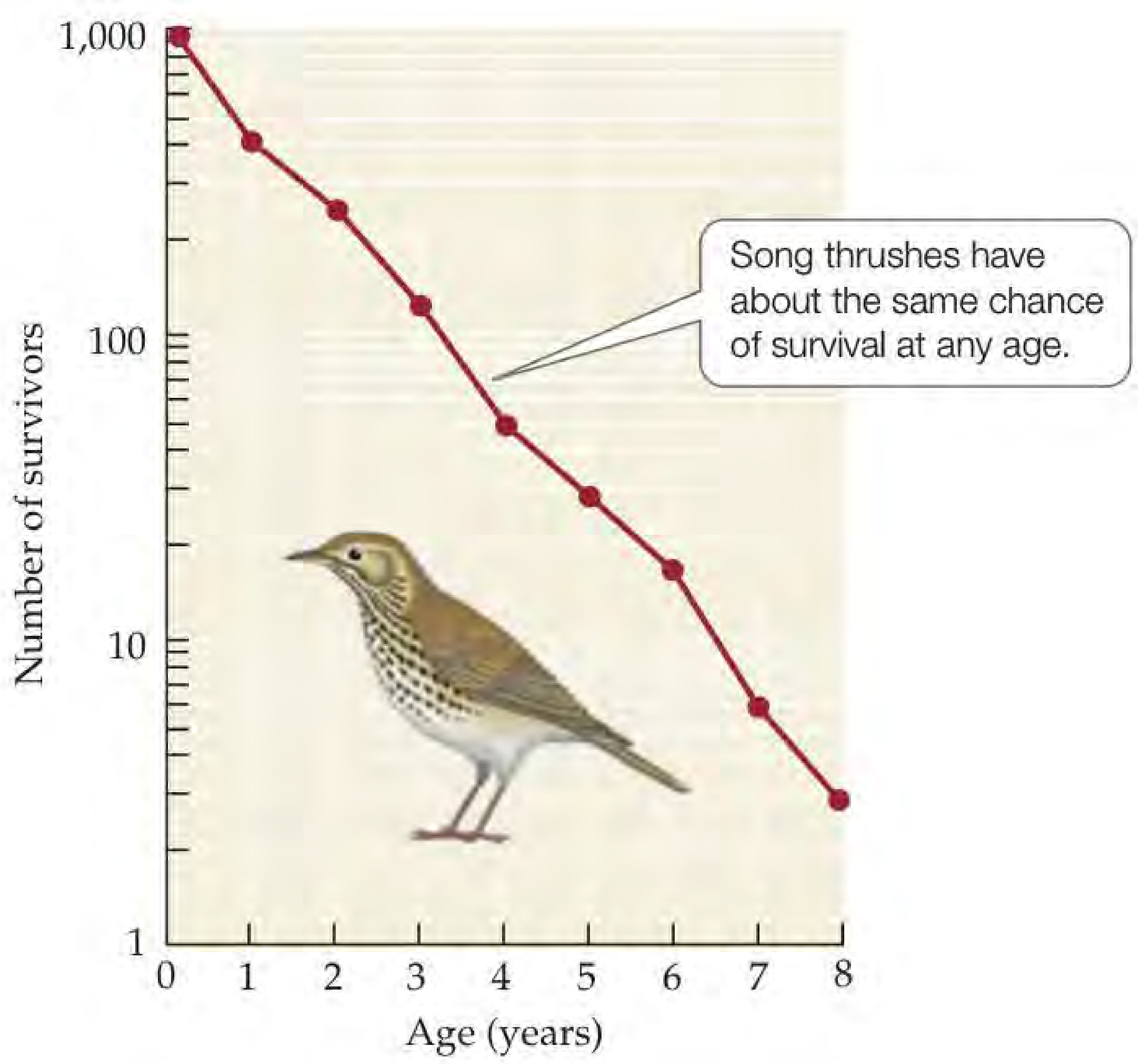
? What percentage of Dall mountain sheep survive to age 11?

(A) Type I



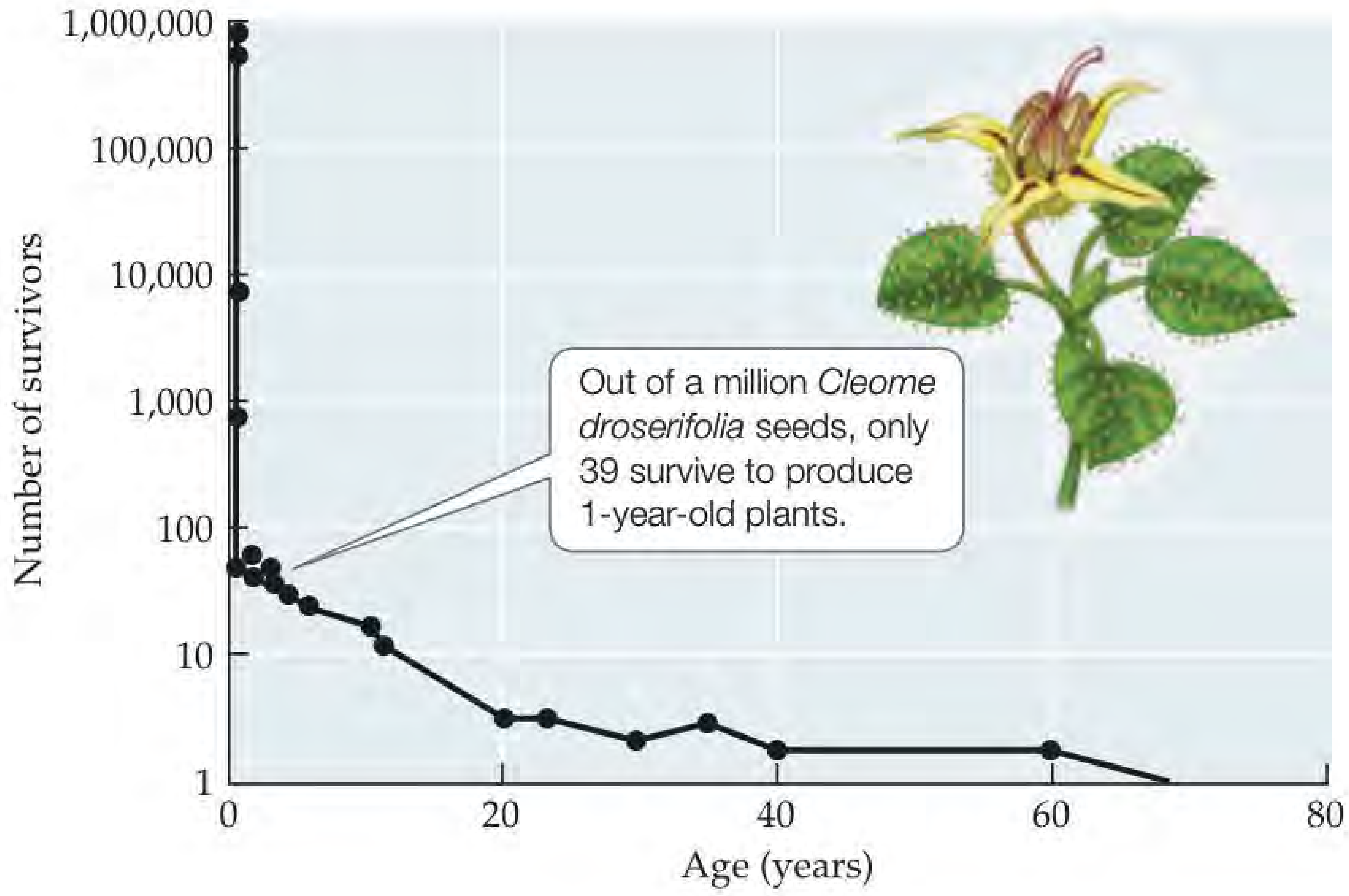
Most Dall mountain sheep survive to old age.

(B) Type II



Song thrushes have about the same chance of survival at any age.

(C) Type III



Out of a million *Cleome droserifolia* seeds, only 39 survive to produce 1-year-old plants.

giant puffballs, oysters, marine corals, most insects, and many plants, including the desert shrub *Cleome droserifolia* (**Figure 10.6C**). In this species, a population of 2,000 adults produces some 20 million seeds each year (roughly 10,000 seeds per adult), but only about 800 of those seeds survive to become juvenile plants.

We have discussed type I–III survivorship curves as if they were constant for each species, but that is not necessarily the case. Survivorship curves can vary among populations of a species, between males and females in a population, and among cohorts of a population that experience different environmental conditions (see Figure 10.4). In fact, by comparing birth and death rates in groups of individuals that experience different conditions, we can assess the effects of those conditions on populations. As we'll see in the next section, we can also use birth and death rates to predict how the size and composition of a population will change over time.

CONCEPT 10.2
Life table data can be used to project the future age structure, size, and growth rate of a population.

Age Structure

Members of a population whose ages fall within a specified range are said to be part of the same *age class*. Age class 1, for instance, might include all individuals who are at least 1 year old but who are not yet 2 years old. Once individuals have been categorized in this way, a population can be described by its **age structure**: the proportions of the population in each age class. Imagine a population of a hypothetical organism in which all members die before they reach 3 years of age. In this population, every individual will be 0 ("newborns," which includes all individuals less than 1 year old), 1, or 2 years old. If there are 100 individuals in the population, and if 20 are newborns, 30 are 1-year-olds, and 50 are 2-year-olds, then the age structure will be 0.2 in age class 0, 0.3 in age class 1, and 0.5 in age class 2.

Age structure influences how rapidly populations grow

Age structure is a key feature of populations, in part because it influences whether a population increases or decreases in size. Consider two human populations of the same size and with the same survival and fecundity rates, but with different age structures. If one of the populations had many people older than 55, while the other had many people between ages 15 and 30, we would expect the second population to grow more rapidly than the first because it contained more individuals of reproductive age. Indeed, human populations that are growing rapidly typically have a greater percentage of people in younger age classes than do populations that are growing slowly or are in decline (**Figure 10.7**). In general, age structure influences how rapidly any population grows—at least initially, as we'll see next by examining a hypothetical life table in some detail.

Age structure and population size can be predicted from life table data

Table 10.3 shows survival rate and fecundity for a population of a hypothetical organism that reproduces in the spring and dies before it reaches 3 years of age. How will the age structure and size of this population change over time?

To answer these questions, we'll represent the number of individuals in age class 0 (the newborns) by n_0, the number in age class 1 (the 1-year-olds) by n_1, and the number in age class 2 (the 2-year-olds) by n_2. Assume

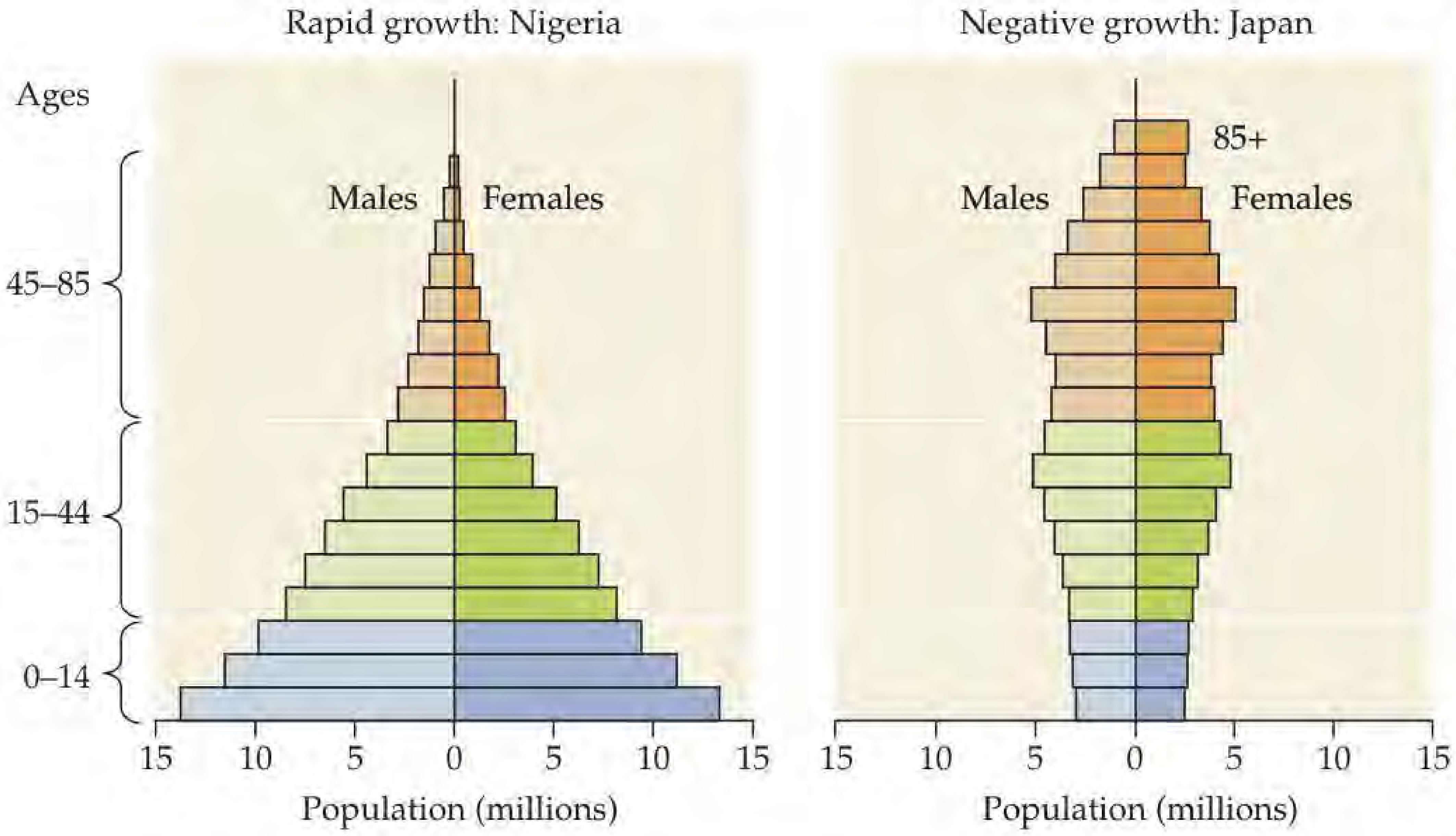


Figure 10.7 Age Structure Influences Growth Rate in Human Populations Population pyramids for Nigeria and Japan show age structures that are typical of human populations with rapidly growing populations (Nigeria) and with growth rates that are negative or close to zero (Japan). The main reproductive ages (15–44) are shown in green. (After Roberts 2011.)

NIGERIA		JAPAN
158	**Population 2010 (millions)**	**127**
5.7	Lifetime births per female	1.4
43	Percentage of population below age 15	13
3	Percentage of population over age 65	23
47	Life expectancy at birth	83
75	Infant mortality (deaths per 1,000 births)	2.6
326	**Projected population 2050 (millions)**	**95**

TABLE 10.3 Life Table for a Hypothetical Organism

AGE, x	SURVIVAL RATE, S_x	SURVIVORSHIP, l_x	FECUNDITY, F_x
0	0.3	1.00	0
1	0.8	0.30	2
2	0.0	0.24	4
3	—	0.0	—

Note: The organism reproduces in the spring and dies before it is 3 years old.

that our population begins with a total of 100 individuals, of which 20 are in age class 0 ($n_0 = 20$), 30 are in age class 1 ($n_1 = 30$), and 50 are in age class 2 ($n_2 = 50$). Assume further that all mortality occurs over the winter, before the next spring breeding season, and that individuals are counted immediately after the breeding season.[1] We can now use the information in Table 10.3 to predict how many individuals our population will have in the following year. To do this, we must calculate two things: (1) the number of individuals that will survive to the next time period (in this case, to the next year's breeding season) and (2) the number of newborns those survivors will produce in the next time period.

To calculate the number of individuals that will survive to the next time period, we multiply the number of individuals in each age class (n_x) by the survival rate (S_x) for that age class (**Table 10.4**). Thus, to determine the number of newborns that will survive to be 1-year-olds in the following year, we multiply $n_0 = 20$ by $S_0 = 0.3$ (see Table 10.3) to get 6 1-year-olds. Similarly, to determine how many of the current 1-year-olds will survive to be 2-year-olds in the following year, we multiply $n_1 = 30$ by $S_1 = 0.8$ to get 24 2-year-olds. Finally, to determine the number of newborns in the following year, we note that, on average, each 1-year-old has 2 offspring and each 2-year-old has 4 offspring (see Table 10.3). Since there will be 6 1-year-olds and 24 2-year-olds in the next year, the number of offspring produced at that time will be $(6 \times 2 + 24 \times 4) = 108$. Thus, in the following year, the total population size (N) will be $N = 138$ (108 newborns + 6 1-year-olds + 24 2-year-olds).

Now that we have predicted how the age structure and size of our hypothetical population will change in one year, we can extend those calculations to future years. Just as we used the data in Table 10.3 to predict that the population would increase from 100 individuals in the first year (at time $t = 0$) to 138 individuals in the next year (at time $t = 1$), we can perform calculations similar to those in Table 10.4 to determine how many individuals will be in each age class at time $t = 2$, then time $t = 3$, then time $t = 4$, and so on. We show the results of such calculations in **Figure 10.8**.

In Figure 10.8A, the numbers of individuals in each age class and in the population as a whole are plotted over time. Examining the curve for total population size (N), we see that with one exception ($t = 2$), the population rises steadily from its initial value of $N = 100$, reaching 1,361 individuals at time $t = 10$. By time $t = 4$, the numbers of individuals in each age class also rise steadily. In the first 3 years of population growth, however, the numbers of individuals in the different age classes vary considerably. For example, from its initial value of 50, n_2 drops to 24 individuals at time $t = 1$ and just 5 individuals at time $t = 2$; n_2 then rises substantially, reaching 136 individuals by time $t = 10$.

By time $t = 8$, the four curves in Figure 10.8A are roughly parallel to one another, indicating that all three age classes—and the total population size, N—are increasing at nearly the same rate from one year to the next. To examine this yearly rate of increase further, we can calculate the ratio of the population size in year $t + 1$, denoted N_{t+1}, to the population size in year t, denoted N_t. This ratio provides a measure of the year-to-year *population growth*

TABLE 10.4 A Two-Step Method for Projecting the Size of the Hypothetical Population in Table 10.3

AGE (x)	CURRENT NUMBER OF INDIVIDUALS OF AGE x (n_x)		STEP 1: ESTIMATE SURVIVORS Number of surviving individuals of age x in the next time period	STEP 2: ADD NEWBORNS Number of individuals of age x in the next time period
0	20	$S_0 = 0.3$		108
1	30	$S_1 = 0.8$	6	6
2	50	$S_2 = 0.0$	24	24
3			0	
Total population size:	100 (current time period)			138 (next time period)

Of these 20 newborns, 6 ($20 \times S_0 = 20 \times 0.3$) survive to become 1-year-olds.

Because $S_2 = 0$, none of the 50 2-year-olds survive to become 3-year-olds.

Each of the 6 1-year-olds has 2 offspring and each of the 24 2-year-olds has 4 offspring …

… so there are 108 [$(6 \times 2) + (24 \times 4)$] newborns.

---

[1] Individuals could also be counted at other times, such as just before the breeding season. Although the calculations in the following paragraphs would be different, the final results would be the same; see Caswell 2001 for more information regarding census times.

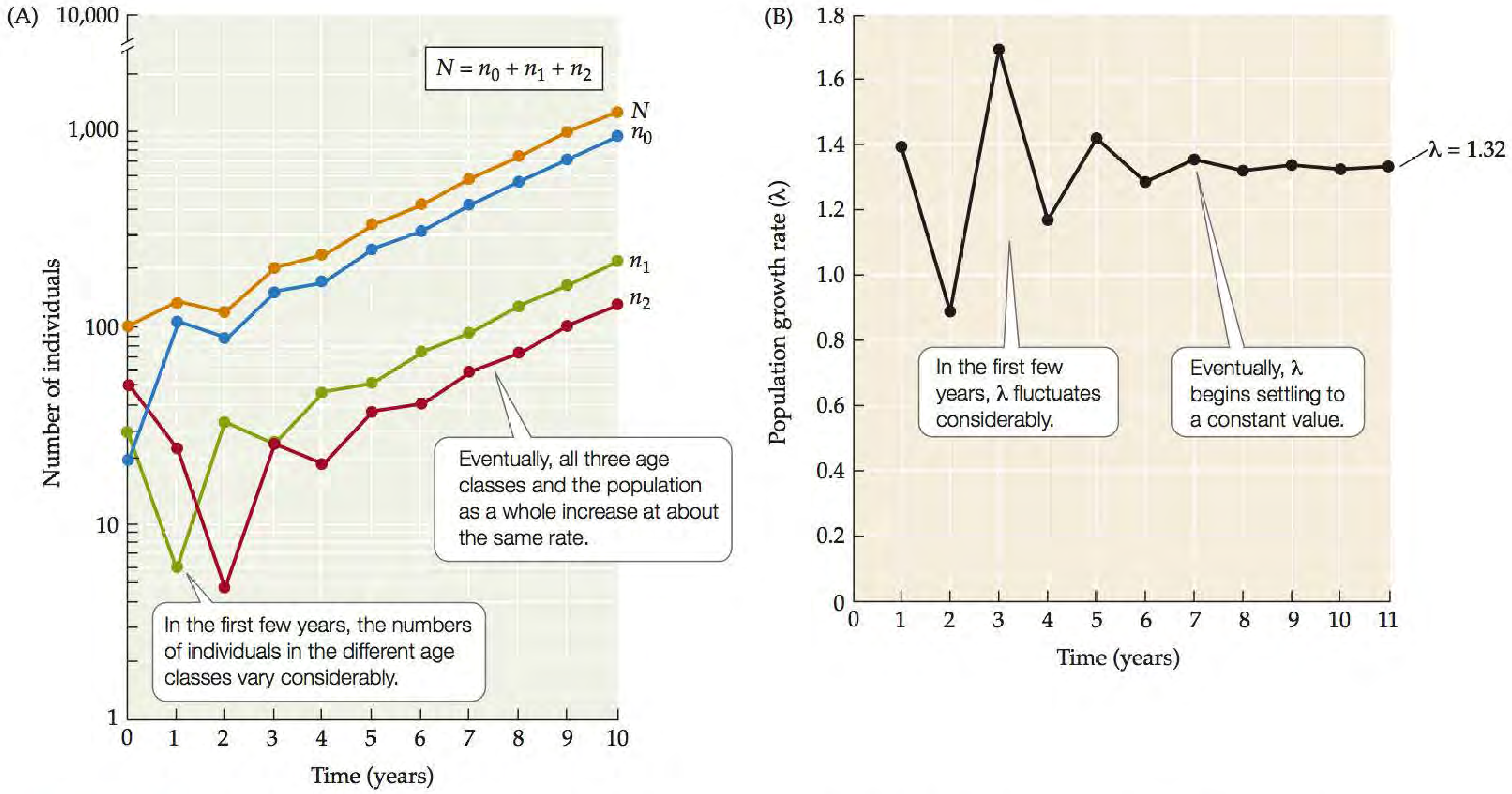


Figure 10.8 Growth of a Hypothetical Population The procedure described in Table 10.4 was used to calculate the growth of the hypothetical population whose life table data are shown in Table 10.3. These graphs plot (A) the number of individuals in each of the three age classes (n_0, n_1, n_2), as well as the total population size (N), at different times, and (B) the yearly population growth rate (λ) for the total population. Note that the number of individuals in (A) is plotted on a log scale.

? Using the graph in (A), estimate λ from year 4 to year 5 for age class 2 (n_2).

rate and is designated by the Greek symbol λ (pronounced "lambda"):

$$\lambda = \frac{N_{t+1}}{N_t}$$

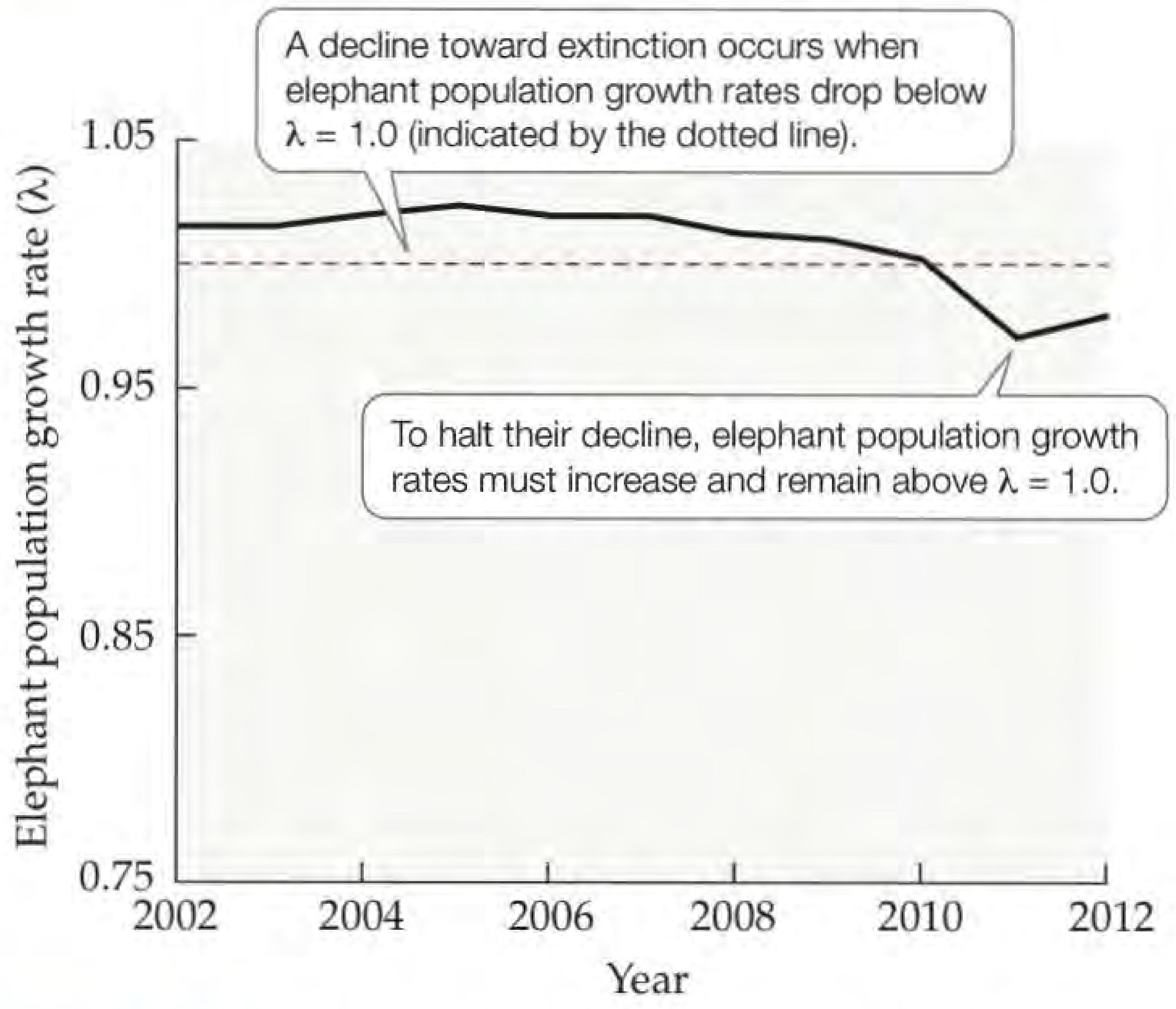
Thus, to determine, for example, how the population will change in size from time $t = 0$ to time $t = 1$, we calculate the ratio of $N_1 = 138$ to $N_0 = 100$, which gives a yearly population growth rate of $\lambda = 1.38$.

As shown in Figure 10.8B, the values for the growth rate λ in our hypothetical population fluctuate over the first few years, ranging from a low of $\lambda = 0.88$ at $t = 2$ to a high of $\lambda = 1.69$ at $t = 3$. Eventually, λ settles to a constant value of $\lambda = 1.32$; if we were to calculate population sizes for additional time periods, we would find that λ remained equal to 1.32 from time $t = 10$ forward. In addition, if we were to calculate λ for any of the age classes [e.g., if we were to calculate the ratio of the size of age class 1 (n_1) at time $t + 1$ to its size at time t], we would find that by time $t = 10$, λ would equal 1.32 for each age class.

Populations grow at fixed rates when age-specific birth and death rates are constant over time

If a population's age-specific survival and fecundity rates are constant over time, that population ultimately grows at a fixed rate from one year to the next. This was the case for our hypothetical population, which eventually grew at the fixed rate of $\lambda = 1.32$ (see Figure 10.8B), as did each of its age classes. Because the population and each of its age classes increase by a constant multiplier every year, the proportion of individuals in each age class remains constant as long as the multiplier (λ) remains constant. When the age structure of a population does not change from one year to the next, the population is said to have a **stable age distribution**. In our example, λ remained constant by year 10, and the number of individuals in each age class at that time (see Figure 10.8A) indicates that the stable age distribution was 0.73 in age class 0, 0.17 in age class 1, and 0.10 in age class 2.

It is important to realize that if the survival and fecundity rates for our hypothetical population were different from those in Table 10.3, we would obtain different values for both the population growth rate (λ) and the stable age distribution. To illustrate this point, we'll change the average number of offspring produced by 1-year-olds (F_1) from 2.0 to 5.07, but keep all other S_x and F_x values equal to those in Table 10.3. With this single change, calculations like those in Table 10.4 show that λ changes from 1.32 to 2.0. This change also alters the stable age distribution to 0.83 in age class 0, 0.12 in age class 1, and 0.05 in age class 2.



A decline toward extinction occurs when elephant population growth rates drop below $\lambda = 1.0$ (indicated by the dotted line).

To halt their decline, elephant population growth rates must increase and remain above $\lambda = 1.0$.

Figure 10.9 **Will Elephants Become Extinct in the Wild?** Population growth rates (λ) for 306 elephant populations show that elephants have been in decline across the African continent since 2010. (After Wittemyer et al. 2014.)

Birth and death rates—and hence population growth rates—can change when environmental conditions change

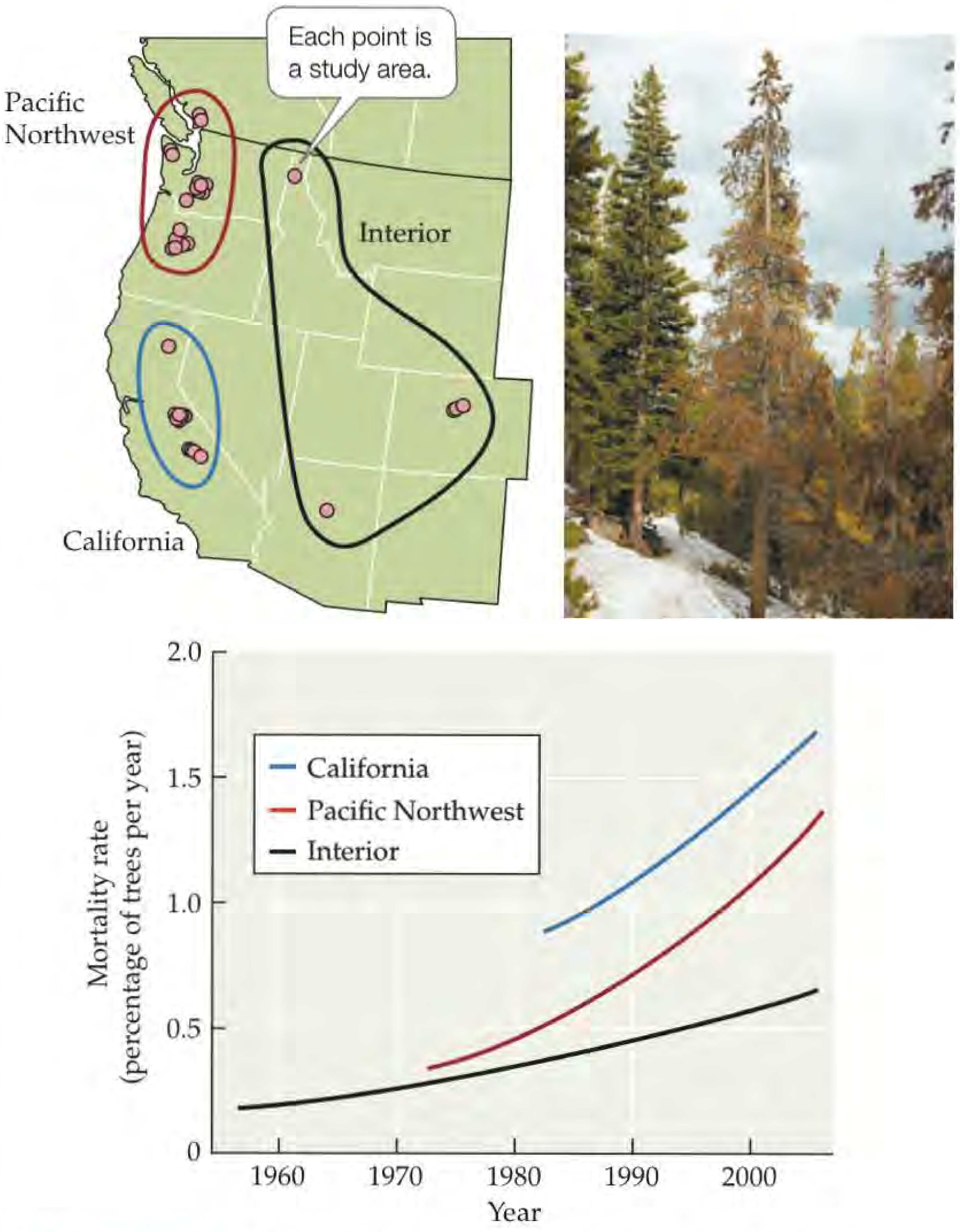
As the effects of our change in F_1 suggest, the growth rate and age structure of a population can change if the age-specific birth or death rates change. Knowing this, ecologists and natural resource managers can seek to modify an organism's biotic or abiotic environment in ways that are intended to change birth or death rates, with the ultimate goal of decreasing the size of a pest population or increasing the size of an endangered population. An efficient way to reach this goal is to identify the age-specific birth or death rates that most strongly influence the population growth rate. In one such example, life table data indicated that the most effective way to increase the growth rates of endangered sea turtle populations was to increase the survival rates of juvenile and mature turtles—a change from the common practice of protecting newborns (**Ecological Toolkit 10.1**).

Even when age-specific birth and death rate data are not available, demographic monitoring programs can be used to identify factors causing population growth rates to rise or fall. For example, in 2002, a system for recording the cause of death of elephants was established in 45 sites across Africa. Wittemyer et al. (2014) combined that information with other demographic data to estimate how elephant population growth rates have changed over time (**Figure 10.9**). Their analyses indicated that across the African continent, elephant population growth rates have dropped below $\lambda = 1.0$, primarily because of a rapid increase in illegal poaching (for tusk ivory) after 2009. For example, 100,000 elephants were killed for ivory over a 3-year period (2010–2012)—a level of illegal killing that cannot be sustained. To prevent elephants from becoming extinct in the wild, elephant population growth rates must increase and remain above $\lambda = 1.0$. For this to occur, new efforts must be taken to curb the rate of illegal killing and reduce the global demand for illegal ivory.

In general, the birth or death rates of a population can be affected by a broad range of abiotic and biotic factors. Sudden changes in environmental conditions can cause rapid and dramatic changes in birth or death rates, as when an increase in hunting or a catastrophic drought causes large-scale die-offs in a population. But birth or death rates can also change more gradually over time, as we'll see in the next example.

CLIMATE CHANGE CONNECTION

Effects of Climate Change on Tree Mortality Rates Over the course of several decades, mortality rates increased gradually in populations of coniferous forest trees across broad regions of the western United States (**Figure 10.10**).

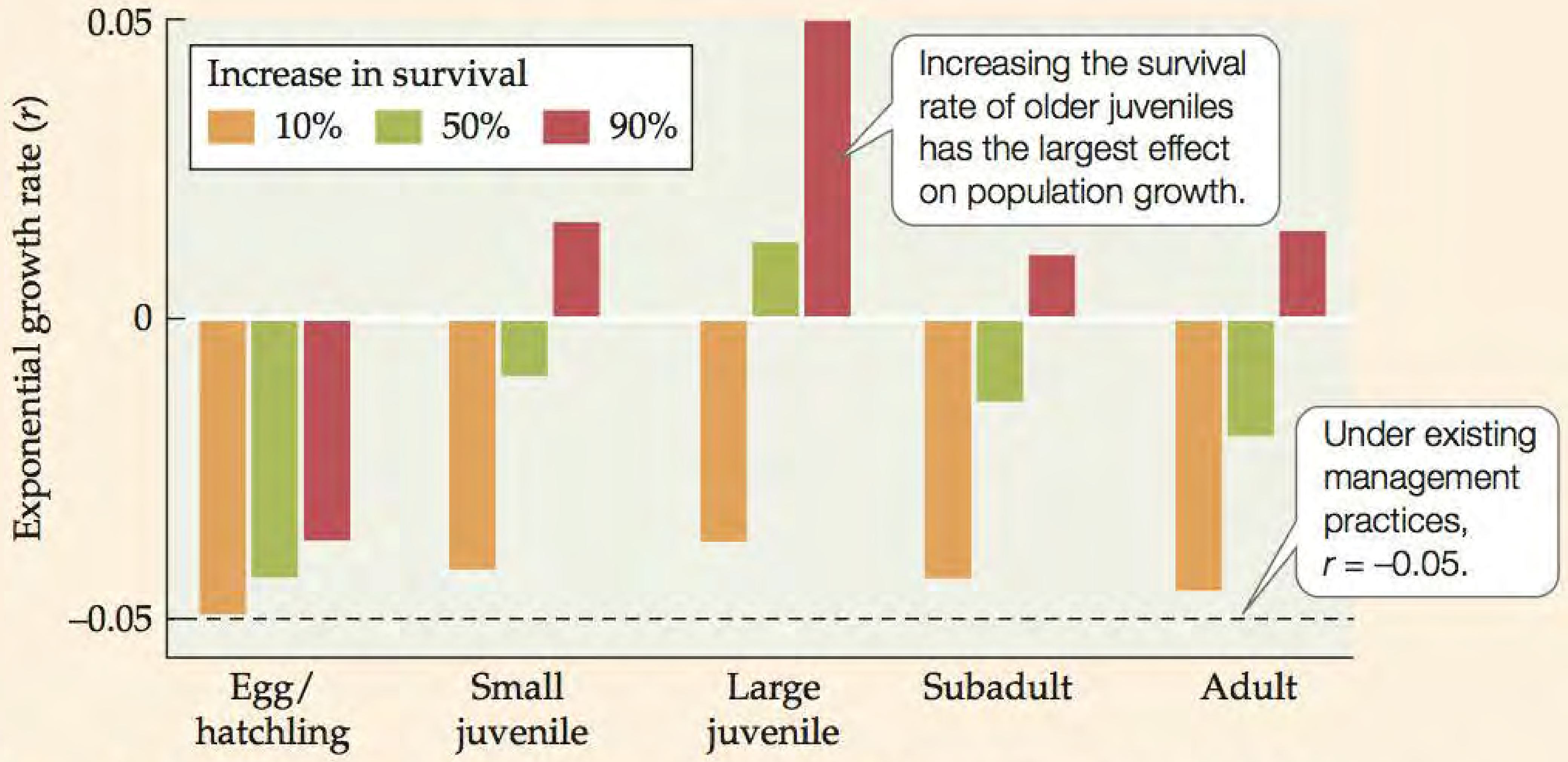


Each point is a study area.

Figure 10.10 **Rising Tree Mortality Rates** Trends in coniferous tree mortality rates for 76 study plots located in the three regions of the western United States shown on the map. (After van Mantgen et al. 2009.)

ECOLOGICAL TOOLKIT 10.1

Estimating Population Growth Rates in a Threatened Species



Increasing the survival rate of older juveniles has the largest effect on population growth.

Under existing management practices, $r = -0.05$.

Figure A **Management Practices and Sea Turtle Population Growth Rates** Researchers used life table data to identify the age-specific death rates that most strongly influenced the population growth rate of loggerhead sea turtles. (After Crowder et al. 1994.)

Loggerhead sea turtles (*Caretta caretta*) are large marine turtles that lay eggs in nests that adult females dig into sandy beaches. Newly hatched baby turtles weigh just 20 g (0.04 pounds) and have a shell length of 4.5 cm (1.8 inches). They reach adulthood after 20–30 years, at which point they can weigh up to 227 kg (500 pounds) and have a shell length of 122 cm (4 feet).

Loggerhead sea turtles have been listed as a threatened species under the U.S. Endangered Species Act since 1978. Many species eat loggerhead eggs or hatchlings, and the juveniles and adults are eaten by large marine predators such as tiger sharks and killer whales. Loggerheads also face threats from people, including the destruction of nesting sites by development, as well as commercial fisheries (in whose nets sea turtles can become trapped and drown).

Early efforts to protect loggerhead sea turtles focused on the egg and hatchling stages, which suffer extensive mortality and are relatively easy to protect. To evaluate this approach, Crouse et al. (1987) and Crowder et al. (1994) used life table data to determine how the existing exponential growth rate of $r = -0.05$ would change if new management practices improved the survival rates of turtles of various ages (**Figure A**). Their findings suggested that even if hatchling survival rates were increased by 90%, loggerhead populations would continue to decline. Instead, they found that the population growth rate was most responsive to increasing the survival rates of older juveniles and adults.

The results obtained by Crouse, Crowder, and their colleagues prompted the enactment of laws requiring turtle excluder devices (TEDs) to be installed in shrimp nets (**Figure B**). A TED functions as a hatch through which juvenile and adult sea turtles can escape when caught in a net. Shrimp nets were singled out because the data suggested that shrimping accounted for more loggerhead deaths (from 5,000 to 50,000 deaths per year) than all other human activities combined.

Loggerheads are most easily counted when they nest, yet it takes 20–30 years for turtles to become sexually mature. As a result, it will be decades before we know whether TED regulations help turtle populations to increase in size. But early results are encouraging: the number of turtles killed in nets dropped substantially (up to 94%) after the TED regulations were implemented (Finkbeiner et al. 2011).

Figure B **Turtle Excluder Device (TED)**

These increases occurred in stands of seemingly healthy forest that had not been cut for more than 200 years, leading researchers to ask, What is killing the trees?

In seeking an answer to this question, Van Mantgem et al. (2009) ruled out several possible causes, including air pollution, forest fragmentation, changes in fire frequency, and within-stand increases in the intensity of competition. The researchers went on to note that during the time period covered by their study, regional temperatures in the western United States had increased at rates of 0.3°C–0.5°C per decade. These rapid temperature increases were associated with declines in the snowpack, earlier spring snowmelt, and a lengthening of the summer dry period. These changes caused an increase in the trees' *climatic water deficit* (the amount by which a plant's annual evaporative demand for water exceeds available water). Previous studies had shown that tree mortality rates tend to increase when climatic water deficit increases (Bigler et al. 2007). Overall, van Mantgem et al.'s study suggests that the rise in tree mortality rates was driven by regional warming and the ensuing drought stress. Similarly, in the southwestern United States, warmer temperatures in the summer and reduced snowfall in the winter have produced "hotter droughts" that are associated with increases in the area burned by wildfires and the area affected by insect outbreaks—again causing tree mortality rates to rise (Williams et al. 2013). (We will continue our discussion of how climate change affects forests in **Online Climate Change Connection 10.1**.) 🌍

CONCEPT 10.3

Populations can grow exponentially when conditions are favorable, but exponential growth cannot continue indefinitely.

Exponential Growth

Many organisms, such as giant puffball fungi and the desert shrub *Cleome droserifolia*, produce large numbers of offspring. In such cases, if even a small fraction of those offspring survive to reproduce, the population can increase in size very quickly. Even populations of people and other organisms that produce relatively few young can grow rapidly. In general, populations can grow rapidly whenever individuals leave an average of more than one offspring over substantial periods of time. In this section, we describe geometric growth and exponential growth, two related patterns of population growth that can lead to rapid increases in population size.

Populations grow geometrically when reproduction occurs at regular time intervals

Some species, such as cicadas and annual plants (and the hypothetical species described in Table 10.3), reproduce in synchrony at regular time intervals. These regular time intervals are called *discrete time periods*. If a population of such a species changes in size by a constant proportion from one discrete time period to the next, **geometric growth** is said to occur. The fact that the population grows by a constant proportion means that the number of individuals added to the population becomes larger with each time period. As a result, the population grows larger by ever-increasing amounts. When plotted on a graph, this growth pattern forms a J-shaped set of points (**Figure 10.11A**).

Mathematically, we can describe geometric growth as

$$N_{t+1} = \lambda N_t \qquad \textbf{(10.1)}$$

where N_t is the population size after t generations or, equivalently, after t discrete time periods (e.g., t years if there is one generation per year), and λ is any number greater than zero. In Equation 10.1, λ serves as a multiplier that allows us to predict the size of the population in the next time period. We'll refer to λ as the **geometric population growth rate**; λ is also known as the (per capita) **finite rate of increase**. We use this terminology by convention, but it can be confusing: we can see from Equation 10.1 that when the population "growth" rate λ is between 0 and 1, the population does not grow, but rather decreases in size over time.

Geometric growth can also be represented by a second equation,

$$N_t = \lambda^t N_0 \qquad \textbf{(10.2)}$$

where N_0 is the initial population size (i.e., the population size at time = 0).

The two equations for geometric growth (Equations 10.1 and 10.2) are equivalent in that each can be derived from the other (see **Web Extension 10.1**). Which one we use depends on what we are interested in. If we want to predict the population size in the next time period and we know λ and the current population size, either equation can be used. If we know the population size in both the current and previous time periods, we can rearrange Equation 10.1 to get an estimate for λ ($\lambda = N_{t+1}/N_t$, as we saw in Concept 10.2). Finally, we can use Equation 10.2 to predict the size of the population after any number of discrete time periods. If $\lambda = 2$, for example, then after 12 time periods, a population that begins with $N_0 = 10$ individuals will have $N_{12} = 2^{12} N_0$ individuals, which (as we can determine by using a calculator with a y^x function) equals 4,096 × 10, or 40,960.

Populations grow exponentially when reproduction occurs continuously

In contrast to the pattern described in the previous section, individuals in many species (including people) do not reproduce in synchrony at discrete time periods; instead, they reproduce at varying times. In such organisms, referred to as *continuously* reproducing species, generations typically overlap. When a population of a

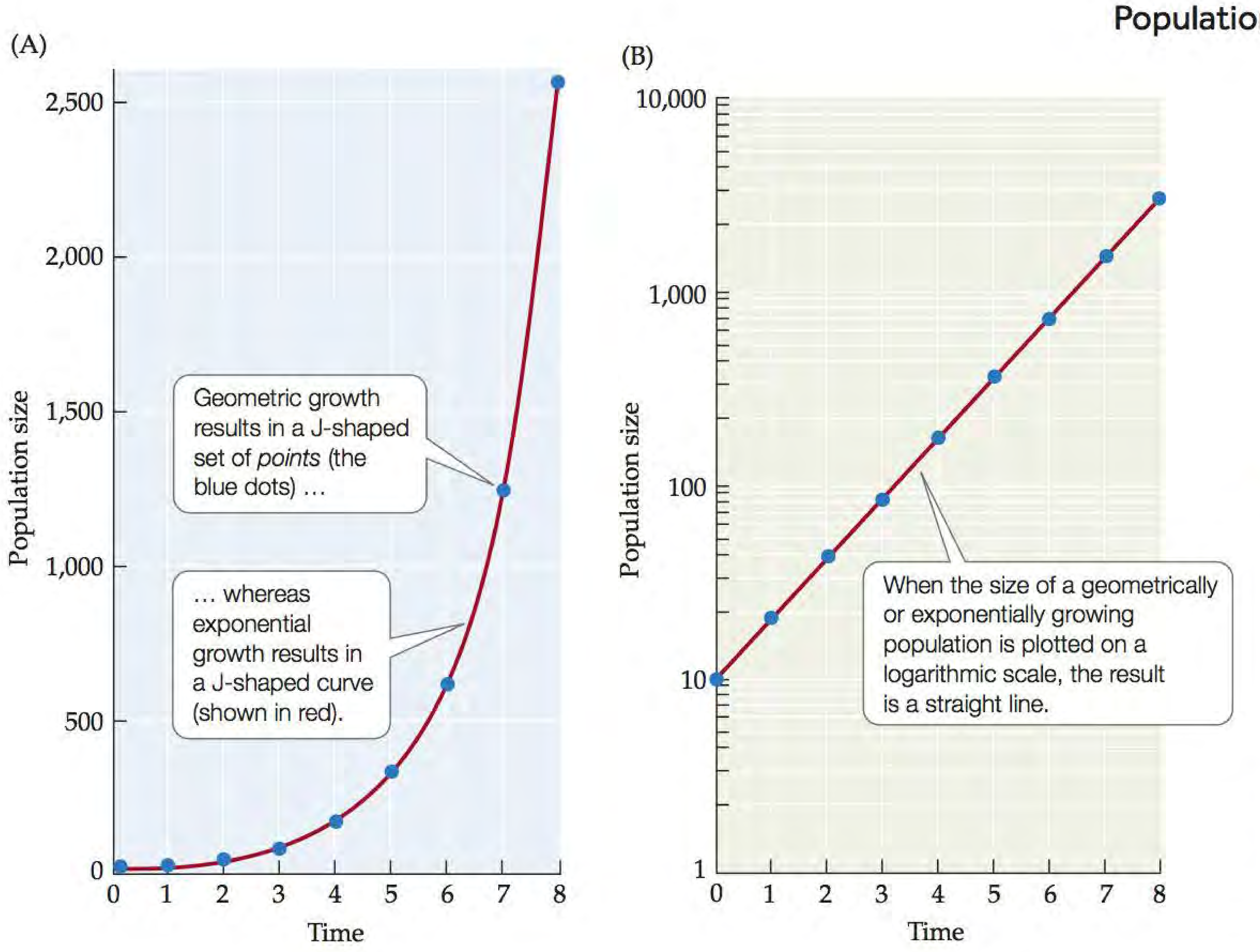


Figure 10.11 Geometric and Exponential Growth (A) The blue dots plot the size of a geometrically growing population that begins with 10 individuals and doubles in each discrete time period (i.e., $N_0 = 10$ and $\lambda = 2$). The red curve plots exponential growth in a comparable population that reproduces continuously, also beginning with 10 individuals and having a growth rate of $r = \ln(2) = 0.69$. (B) When the population sizes represented by the blue circles and the red curve in (A) are plotted on a logarithmic scale, the result is a straight line.

species with continuous reproduction changes in size by a constant proportion at each instant in time, we refer to the growth that results as **exponential growth** (see the red curve in Figure 10.11A). Mathematically, exponential growth can be described by the following two equations:

$$\frac{dN}{dt} = rN \tag{10.3}$$

and

$$N(t) = N(0)e^{rt} \tag{10.4}$$

where $N(t)$ is the population size at each instant in time, t.

In Equation 10.3, dN/dt represents the rate of change in population size at each instant in time; we see from the equation that dN/dt equals a constant rate (r) multiplied by the current population size, N. Thus, the multiplier r provides a measure of how rapidly a population can grow; r is called the **exponential growth rate** or the (per capita) **intrinsic rate of increase**.

As we did for Equation 10.2, we can use Equation 10.4 to predict the size of an exponentially growing population at any time t, provided we have an estimate for r and know $N(0)$, the initial population size. The "e" in Equation 10.4 is a constant, approximately equal to 2.718 ["e" is the base of the natural logarithm, $\ln(x)$]. We can calculate e^{rt} using the function e^x, which can be found on many calculators.

When plotted on a graph, the exponential growth pattern forms a curve that, like the geometric growth pattern, is J-shaped. Exponential growth and geometric growth are similar in that we can draw an exponential growth curve through the discrete points of a population that grows geometrically (see Figure 10.11A). Because exponential and geometric growth curves overlap, both types of growth are sometimes lumped together for simplicity and referred to as *exponential growth*.

Geometric and exponential growth curves overlap because Equations 10.2 and 10.4 are similar in form, except that λ in Equation 10.2 is replaced by e^r in Equation 10.4. Thus, if we want to compare the results of discrete time and continuous time growth models, we can calculate λ from r, or vice versa:

$$\lambda = e^r$$

$$r = \ln(\lambda)$$

where $\ln(\lambda)$ is the natural logarithm of λ, or $\log_e(\lambda)$. For example, if $\lambda = 2$ (as in Figure 10.11A), an equivalent value for r would be $r = \ln(2)$, which is approximately 0.69. **Figure 10.11B** illustrates a simple way to determine whether a population really is growing geometrically (or exponentially): plot the natural logarithm of population size versus time, and if the result is a straight line, the population is increasing by geometric or exponential growth.

Finally, look again at Equations 10.1 and 10.3. In Equation 10.1, which value of λ will ensure that the population does not change in size from one time period to the next? Similarly, in Equation 10.3, which value of r causes the population to remain fixed in size? The answers are $\lambda = 1$ (because then $N_{t+1} = N_t$) and $r = 0$ (because then the rate at which the population size changes is 0). When $\lambda < 1$ (or $r < 0$), the population will decline to extinction, whereas when $\lambda > 1$ (or $r > 0$), the population will increase exponentially (or geometrically) to form a J-shaped curve (**Figure 10.12**).

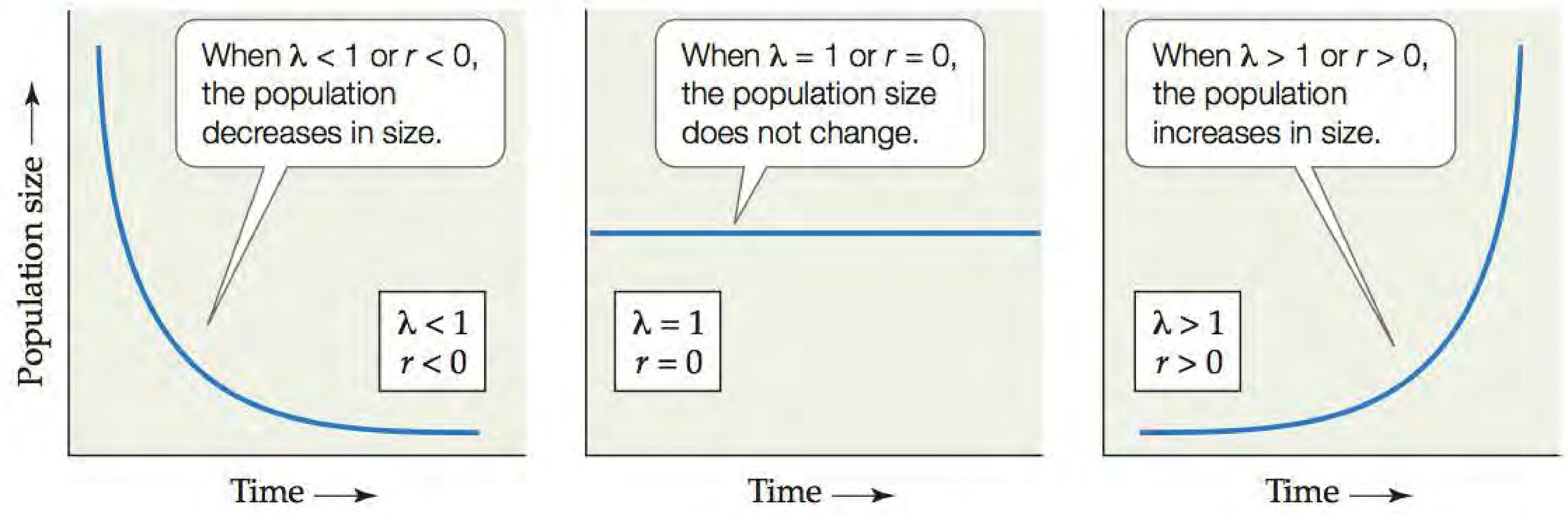


Figure 10.12 How Population Growth Rates Affect Population Size Depending on the value of λ or *r*, a population with an exponential growth pattern will decrease in size, remain the same size, or increase in size.

How can we estimate a population's growth rate (*r* or λ)? In one approach, Equation 10.4 is used to estimate the growth rate *r* at different points in time, as you can explore for the human population in **Analyzing Data 10.1**. There are a variety of other methods as well (see Caswell 2001), including one that we discussed in Concept 10.2: use life table data to predict future population sizes, graph those predicted population sizes versus time, and estimate the growth rate (λ) from the graph. Ecologists often estimate λ (or *r*) from life table data, since they can then determine how fast a population is growing. Life table data can also be used to calculate two other measures of population growth: the doubling time and the net reproductive rate.

Doubling times and net reproductive rates provide useful measures of population growth

The **doubling time** (t_d) of a population is the number of years it will take the population to double in size. As interested readers can confirm [by solving Equation 10.4 for the time it takes a population to increase from its initial size, $N(0)$, to twice that size, $2N(0)$], doubling times can be estimated as

$$t_d = \frac{\ln(2)}{r} \qquad (10.5)$$

where *r* is the exponential growth rate.

As we've seen, *r* (and hence t_d) can be estimated from life table data. We can also use life table data (broken down by age class) to calculate the **net reproductive**

ANALYZING DATA 10.1 How Has the Growth of the Human Population Changed over Time?

Ecologists often use estimates of λ or *r* to determine how rapidly a population is growing (or declining) at various points in time. For a population that is growing exponentially, we can calculate such estimates by rearranging Equation 10.4 to read

$$e^{rt} = \frac{N(t)}{N(0)}$$

where *N*(0) is the population size at the beginning of a time period, *t* is the length of the time period, and *N*(*t*) is the population size at the end of the period. If we know *t*, *N*(0), and *N*(*t*), we can then estimate *r*:

$$r = \frac{\ln\left(\frac{N(t)}{N(0)}\right)}{t}$$

In this exercise, we'll use this technique and the data in the table to examine the growth rate of the world's human population at different points in time.

1. Calculate the exponential growth rates for the years shown in the table. For example, from year 1 to year 400, the length of the time period, *t*, is *t* = 400 – 1 = 399, and we find that *r* = [ln(190 million/170 million)]/399 = 0.1112/399 = 0.00028.
2. If the human population continued to grow at the rate you calculated for 2010, how large would the population be in 2060? (Some of you will retire at about that time.)
3. What assumptions did you make in answering question 2? Based on results for Question 1, is it likely that the human population will reach the size that you calculated for 2060? Explain.

YEAR (C.E.)	POPULATION SIZE	EXPONENTIAL GROWTH RATE (*r*)
1	170 million	0.00028
400	190 million	?
800	220 million	?
1200	360 million	?
1550	500 million	?
1825	1 billion	?
1930	2 billion	?
1960	3 billion	?
1999	6 billion	?
2010	6.87 billion	?
2016	7.35 billion	(NA)

See the companion website for a similar ANALYZING DATA exercise.

rate (R_0): the mean number of offspring produced by an individual during its lifetime. R_0 is calculated as

$$R_0 = \sum_{x_{\text{first}}}^{x_{\text{last}}} l_x F_x \qquad \textbf{(10.6)}$$

where x is age, x_{first} is the age of first reproduction, x_{last} is the age of last reproduction, and l_x and F_x are survivorship and fecundity, respectively, as defined in Table 10.1. Note that to estimate R_0, we multiply by l_x because the likelihood of surviving to each reproductive age is just as important as the number of offspring produced at that age (F_x). To check your understanding of Equation 10.6, use Table 10.1 to calculate an estimate of R_0 for the grass *Poa annua*; your calculations should yield $R_0 = 845.9$.

Whenever R_0 is greater than 1, measured from one generation to the next, λ will be greater than 1 (and $r > 0$). Under these conditions, populations have the potential to increase greatly in size, as we'll see in the next section.

Populations can grow rapidly because they increase by multiplication

Equations 10.1 and 10.3 show that populations increase by multiplication, not addition: at each point in time, the population changes in size according to the multiplier λ or r. As a result, populations have the potential to add large numbers of individuals rapidly whenever $\lambda > 1$ or $r > 0$. The principle at work here is the same one that applies to interest on a savings account. Even when the interest rate is low, you can earn a lot of money each year if you have a large amount deposited in the bank, because savings, like populations, grow by multiplication. Similarly, the fact that populations grow by multiplication means that even a low growth rate can cause the size of a population to increase rapidly.

Consider our own population. In this chapter's Case Study, we stated that the current annual growth rate of the human population was 1.1%. Such a growth rate implies that $\lambda = 1.011$, and hence that $r = \ln(\lambda) = 0.0109$, a value that seems close to 0. If we set the year 2016 as time $t = 0$, we have $N(0) = 7.35$ billion, the size of the human population in 2016. Plugging these values of r and $N(0)$ into Equation 10.4, we calculate that the population size 1 year later should be $N(1) = 7.35 \times e^{0.0109}$, which equals 7.43 billion people. Thus, in 2016, the human population was increasing by 80 million people per year (7.43 billion – 7.35 billion = 0.08 billion = 80 million). Since populations grow by multiplication, if r remained constant at 0.0109 for an extended period of time, the yearly increments to the human population would become astronomical. For example, after 225 years, there would be over 85 billion people, and our population would be increasing in size by almost a billion people *each year*.

Turning from humans to other species, what do field studies reveal about the growth rates of their populations? Some species, such as the woodland herb *Asarum canadense* (wild ginger), have maximum observed values of λ that are close to 1 ($\lambda = 1.01$ in young forests, $\lambda = 1.1$ in mature forests) (**Figure 10.13**). Similar values were observed for a population of 25 reindeer introduced to Saint Paul Island off the coast of Alaska in 1911. After 27 years, the population had increased from 25 to 2,046 individuals, which (when we solve for λ in Equation 10.2) yields $\lambda = 1.18$.

Considerably higher annual growth rates have been observed for populations of many species, including western gray kangaroos ($\lambda = 1.9$), field voles ($\lambda = 24$), and rice weevils ($\lambda = 10^{17}$), which are insect pests of rice and other grains. Some bacteria, such as the mammalian gut inhabitant *E. coli*, can double in number every 30 minutes, resulting in the unimaginably high annual growth rate of $\lambda = 10^{5,274}$.

Recall that when $\lambda > 1$ (or $r > 0$) for an extended period, populations increase exponentially in size, forming a J-shaped curve like that in Figure 10.11A. In natural populations, $\lambda > 1$ (or $r > 0$) when key factors in the environment are favorable for growth, survival, and reproduction. But can such favorable conditions last for long?

There are limits to the growth of populations

An argument from basic principles suggests that the answer to the question we just posed is no. Physicists estimate that the known universe contains a total of 10^{80} atoms. Yet

YEAR	POPULATION GROWTH RATE (λ)
1990–1991	0.80
1991–1992	0.77
1992–1993	0.82
1993–1994	1.01
1994–1995	0.96

Figure 10.13 Some Populations Have Low Growth Rates The growth rates of a population of wild ginger (*Asarum canadense*) in a young forest vary from year to year. The maximum growth rate in this forest is 1.01. However, growth rates are often less than 1.0, suggesting that the population will decline in size unless conditions improve. (Data from Damman and Cain 1998.)

if favorable conditions persisted for long enough, allowing λ to remain greater than 1, even populations of relatively slowly growing species would eventually increase to more than 10^{80} individuals. For example, based on *Asarum*'s growth rate of $\lambda = 1.01$ in young forests, a population that began with 2 plants would have more than 10^{82} plants after 19,000 years. For an extremely rapidly growing species such as *E. coli*, the numbers are even more absurd: it would take only 6 days for a population that began with a single bacterium to exceed 10^{80} individuals.

No population could ever come close to having 10^{80} individuals, because there would be no atoms with which to construct their bodies. Thus, exponential growth cannot continue indefinitely. While this is an extreme example (because other difficulties would be encountered long before there was a shortage of atoms), it illustrates a fundamental point: there are limits to population growth, which cause it to slow and eventually stop. We'll look at some of those limits in the following section.

CONCEPT 10.4

Population size can be determined by density-dependent and density-independent factors.

Effects of Density

Although $\lambda > 1$ for all populations under favorable conditions (leading to exponential growth), conditions in nature are rarely favorable for long. For example, Damman and Cain (1998) calculated the geometric growth rate (λ) in each of 5 years for a population of the woodland herb *Asarum canadense* located in a young forest. As mentioned above, the maximum growth rate was $\lambda = 1.01$. During the other 4 years, however, values for λ ranged from 0.77 to 0.96 (see Figure 10.13). Thus, far from threatening to overrun the planet with its offspring, we would expect this population to decline in the long run, unless conditions changed for the better.

What factors cause λ to fluctuate over time? We can explore answers to this question by asking whether the growth rate changes independently of density or as a function of density.

Density-independent factors can determine population size

In many species, year-to-year variation in weather leads to dramatic changes in abundance and hence in population growth rates. For example, Davidson and Andrewartha (1948) studied how weather in Adelaide, Australia, affected populations of the insect *Thrips imaginis*, a pest of roses. By correlating weather conditions with thrips population sizes over a 14-year period, they showed that yearly fluctuations in population size could be predicted accurately by an equation that used temperature and rainfall data (**Figure 10.14**).

Factors such as temperature and precipitation, as well as catastrophic events such as floods or hurricanes, are often referred to as **density-independent** factors, meaning that their effects on birth and death rates are independent of the number of individuals in the population. Likewise, population growth rates (λ or *r*) are density-independent when they are not a function of population density (**Figure 10.15A**).

As the *T. imaginis* data suggest, density-independent factors can have major effects on population size from one year to the next. In principle, such factors could account entirely for year-to-year fluctuations in the size of a population. But density-independent factors do not tend to increase the size of populations when they are small and decrease the size of populations when they are large. A factor that did consistently lead to such changes would cause the population growth rate to change as a function of density—that is, to be density-*dependent*, not density-independent.

Density-dependent factors regulate population size

Limited amounts of factors such as food or space can influence population size in a **density-dependent** manner, which means that they cause birth rates, death rates, or dispersal rates to change as the density of the population changes (**Figure 10.15B**). As densities increase, it is common for birth rates to decrease, death rates to increase, and dispersal from the population (emigration) to increase—all of which tend to decrease population size. When densities decrease, the opposite occurs: birth rates tend to increase and death and emigration rates decrease.

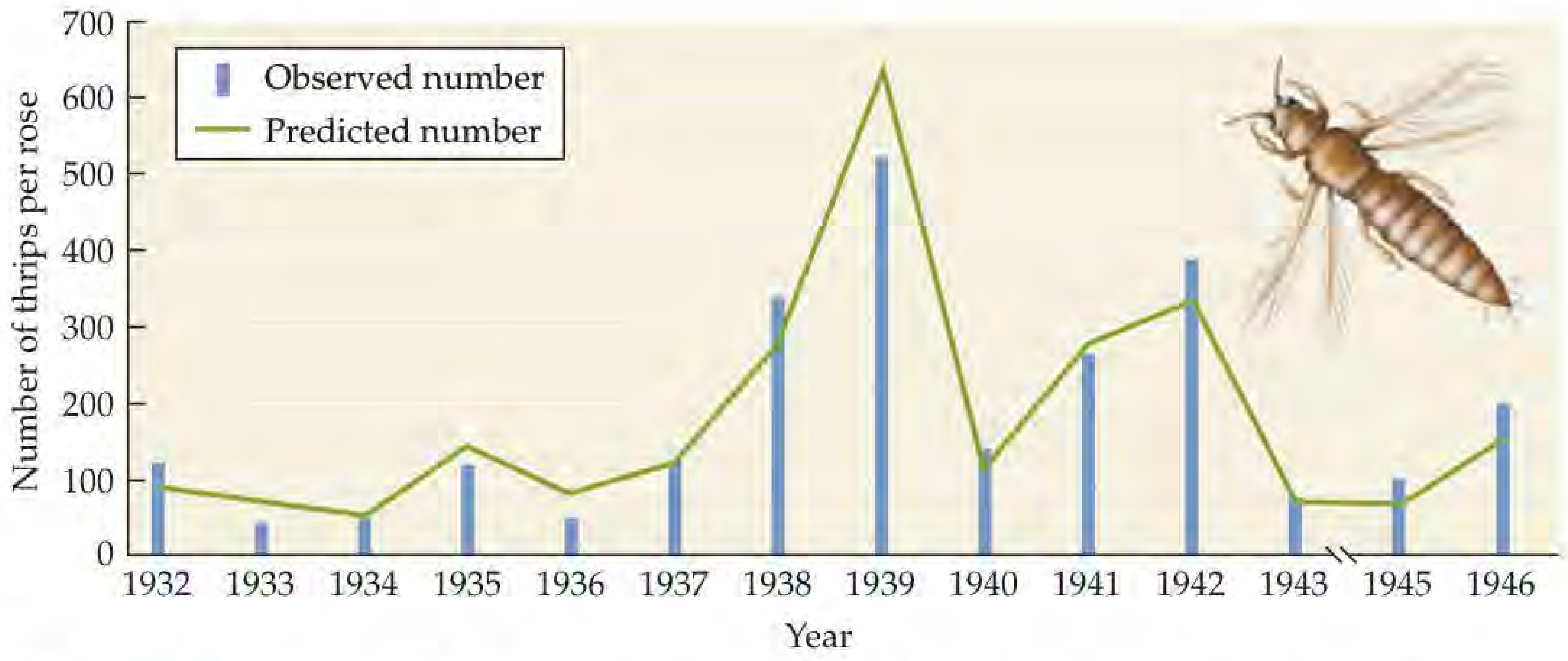


Figure 10.14 Weather Can Influence Population Size Davidson and Andrewartha accurately predicted the mean number of thrips per rose observed in Adelaide, Australia, using an equation based on four weather-related variables. (After Davidson and Andrewartha 1948.)

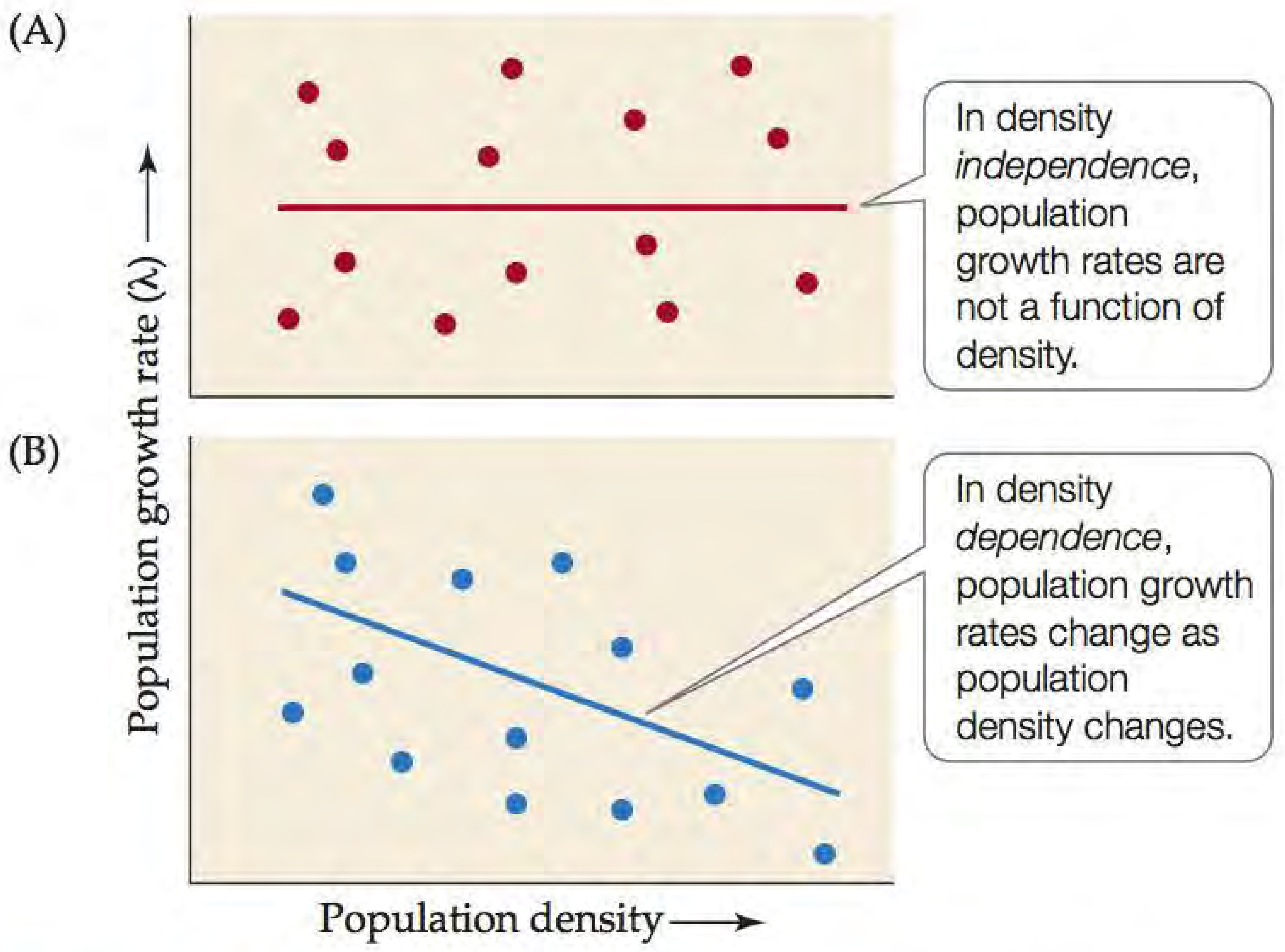
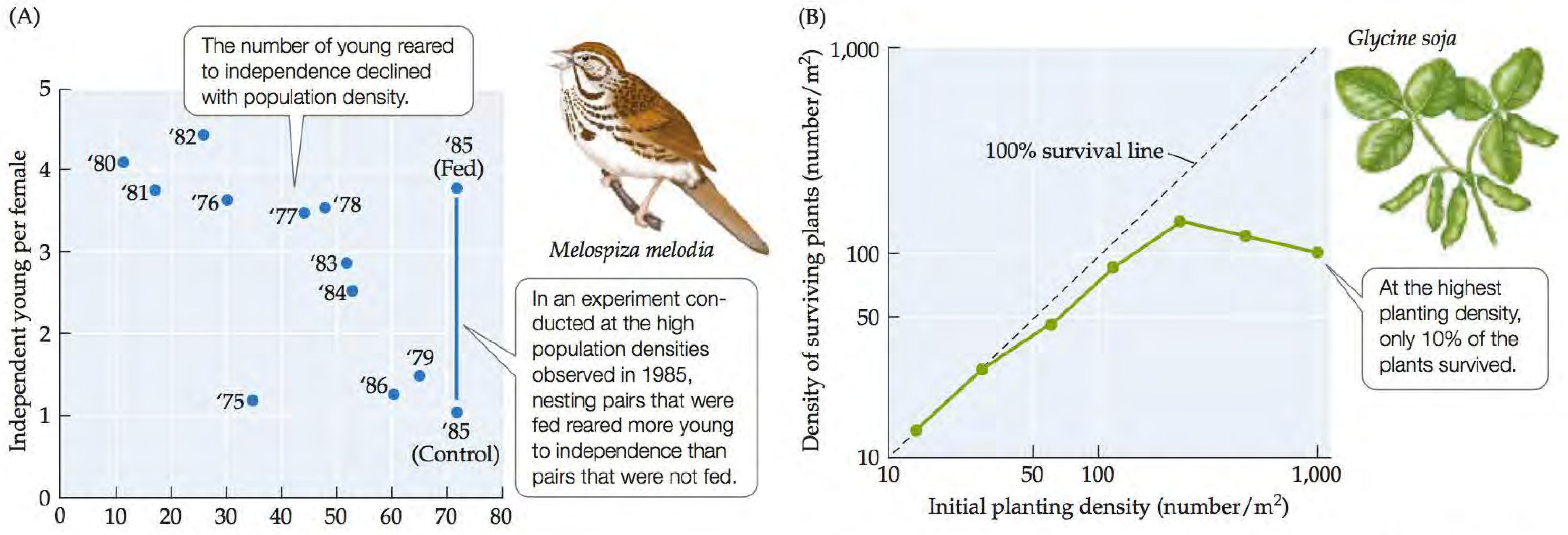


Figure 10.15 Comparing Density Dependence and Density Independence Each point represents one population. (A) Density independence. (B) Density dependence. In this example, population growth rates decrease as population density increases.

When one or more density-dependent factors cause population size to increase when numbers are low and decrease when numbers are high, **population regulation** is said to occur. Ultimately, when the density of any species becomes high enough, density-dependent factors decrease population size because food, space, or other essential resources are in short supply. Note that "regulation" has a particular meaning here, referring to the effects of factors that tend to increase λ or *r* when the population size is small and decrease λ or *r* when the population size is large. Density-independent factors can have large effects on population size, but they do not *regulate* population size because they do not consistently increase population size when it is small and decrease population size when it is large. Thus, by definition, only density-dependent factors can regulate population size.

Density dependence has been observed in many populations

Density dependence can often be detected in natural populations (**Figure 10.16**). For example, in a study that combined field observations with controlled experiments, Peter Arcese and James Smith (1988) examined the effect of population density on reproduction in the song sparrow (*Melospiza melodia*) on Mandarte Island, British Columbia. They found that the number of eggs laid per female decreased with density, as did the number of young that survived long enough to become independent of their parents (see Figure 10.16A). Because Mandarte Island is



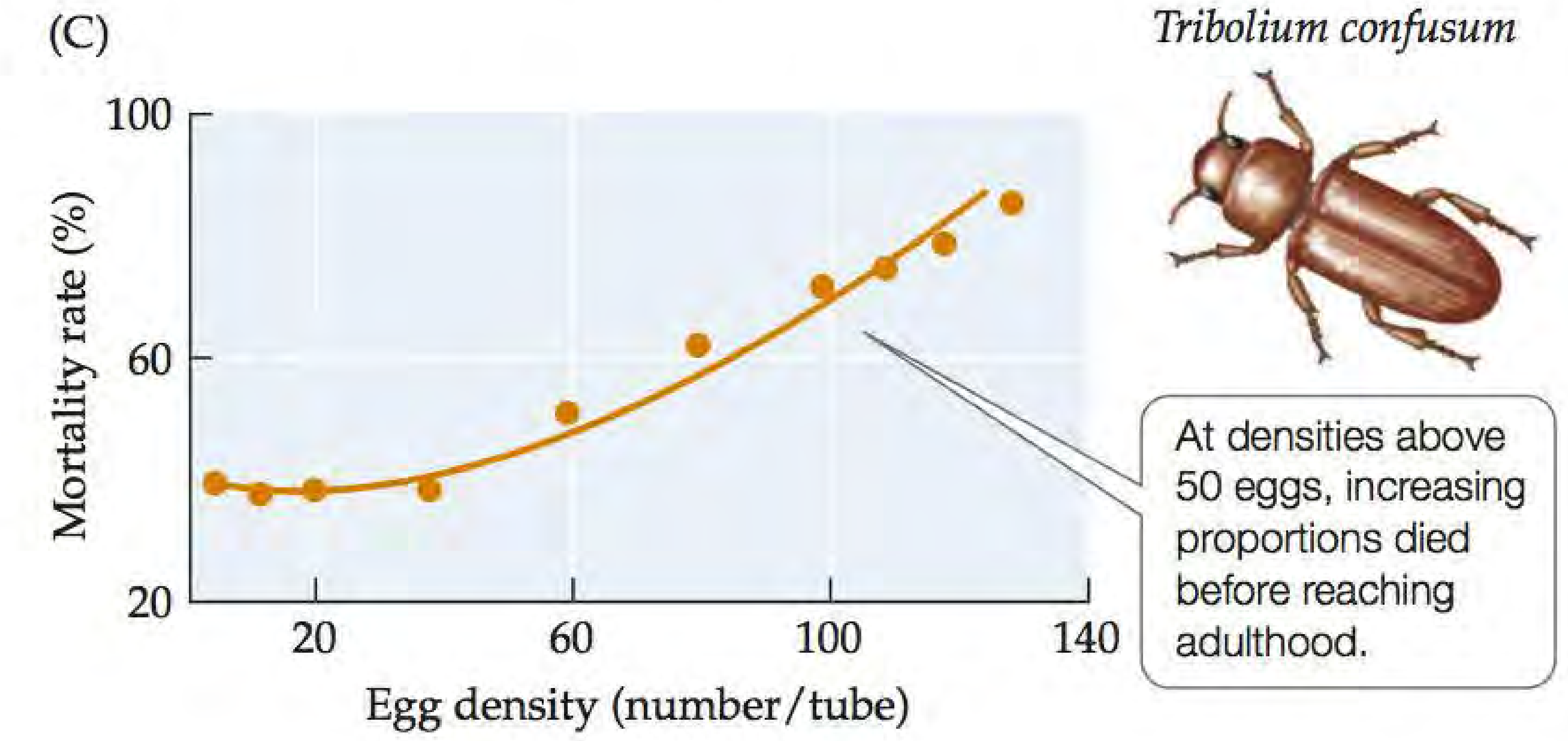
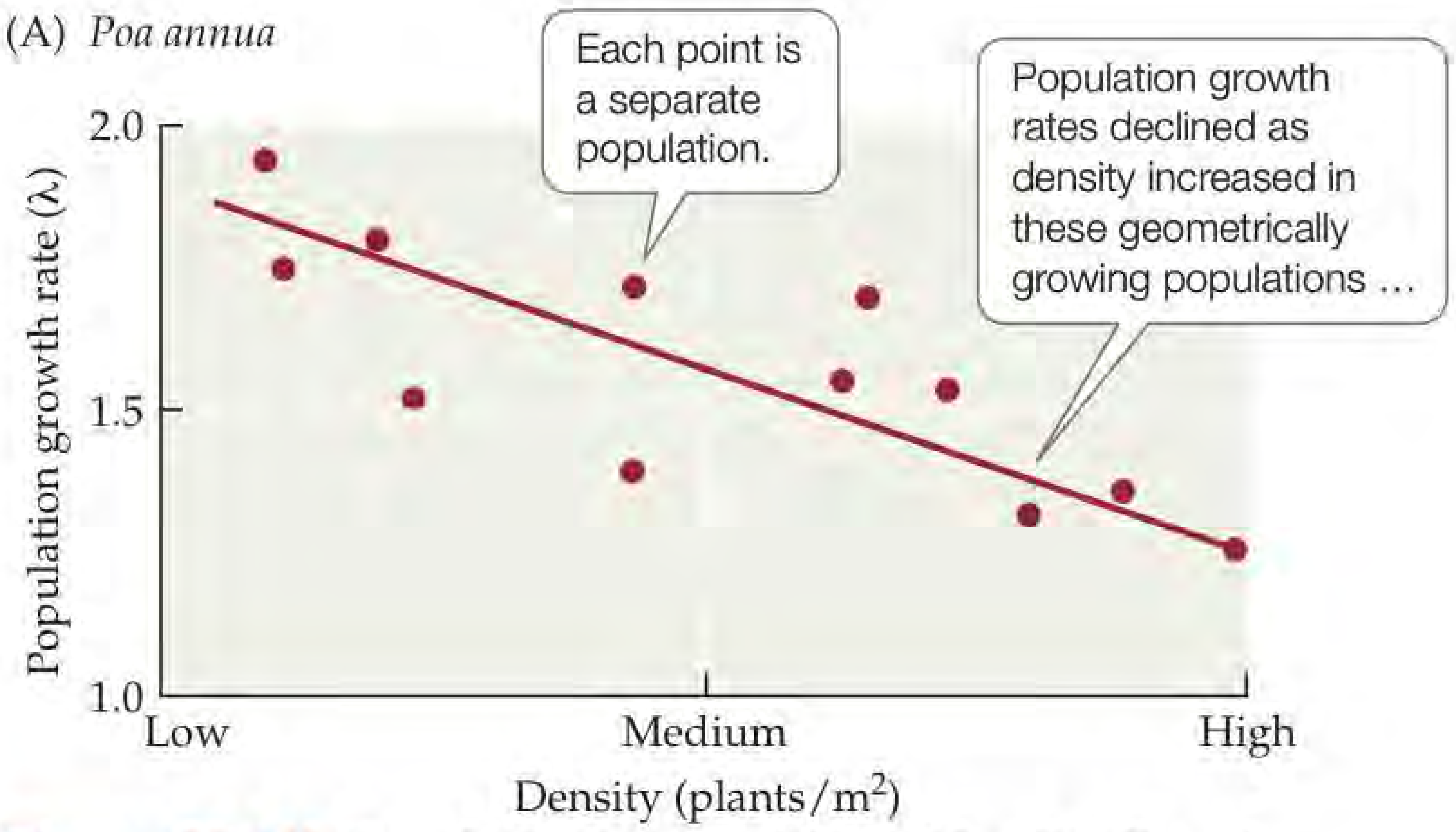


Figure 10.16 Examples of Density Dependence in Natural Populations (A) Numbers of young song sparrows reared to independence on Mandarte Island at different densities of breeding females. The number next to each point indicates the year of observation (1975–1986). (B) Density of surviving soybeans 93 days after they were planted at densities ranging from 10 to 1,000 seeds per square meter. (C) Mortality rates in flour beetles at various egg densities. (A after Arcese and Smith 1988; B after Yoda et al. 1963; C after Bellows 1981.)

? In (A), based on data from years other than 1975, how many young song sparrows per female would you have expected to have been reared to independence in 1975? Explain your reasoning and describe factors that could have caused the observed results.



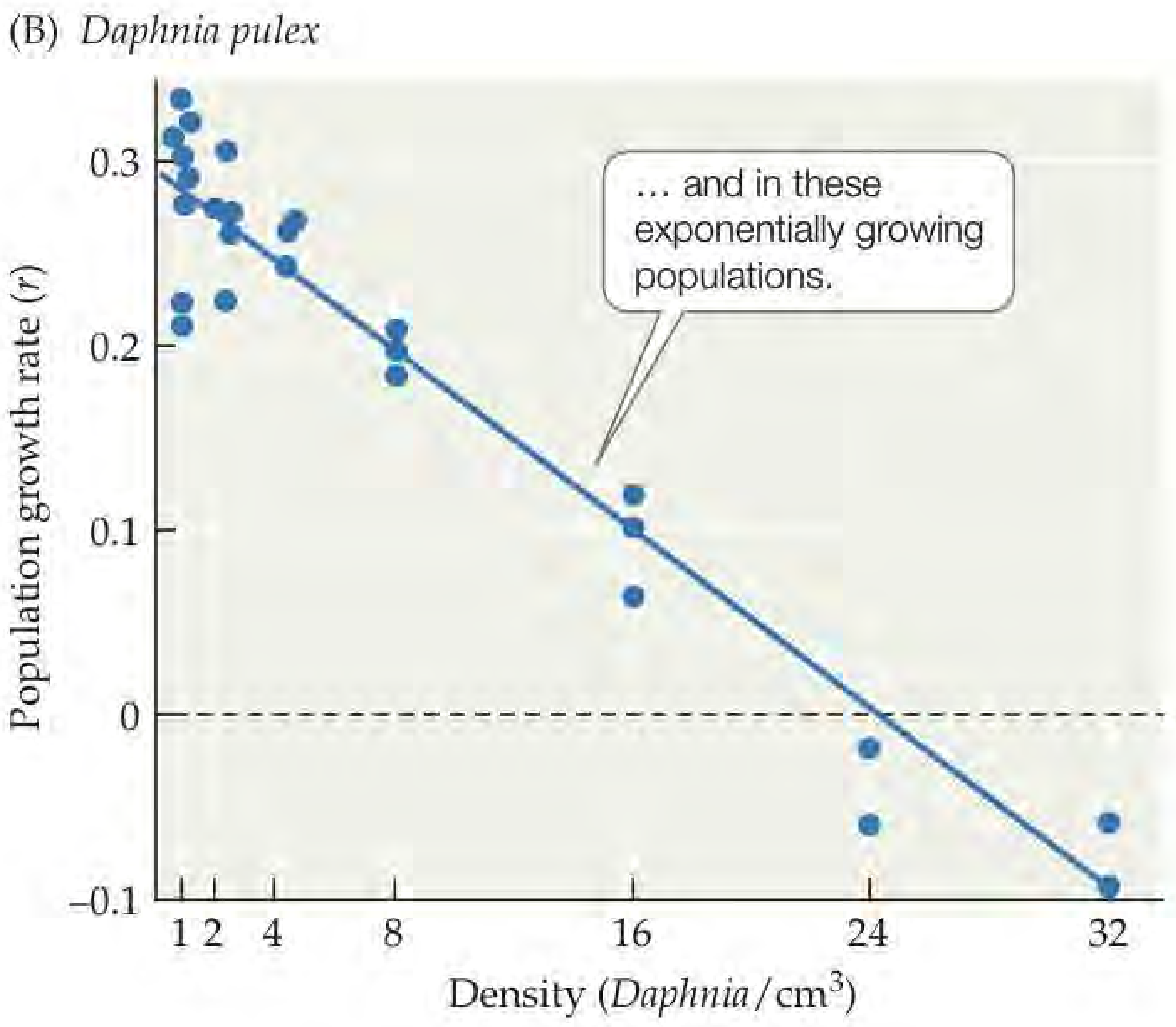


Figure 10.17 Population Growth Rates May Decline at High Densities Each point represents one population. (A) The geometric population growth rate (λ) of the grass *Poa annua* is density-dependent, as is (B) the exponential growth rate (*r*) of the water flea *Daphnia pulex*. (A after Law 1975; B after Frank et al. 1957.)

? Are high-density populations increasing in size in (A)? In (B)? Explain.

small and the birds were likely to suffer food shortages at high densities, Arcese and Smith predicted that if they provided food to a subset of nesting pairs when densities were high, the birds that were fed should be able to rear more young to independence. That is exactly what happened: nesting pairs that were fed reared nearly four times as many young to independence as did control birds that were not fed (see Figure 10.16A).

In addition to density-dependent reproduction, density-dependent mortality has been observed in many populations. For example, when Yoda et al. (1963) planted soybeans (*Glycine soja*) at various densities, they found that at the highest initial planting densities, many of the seedlings had died by 93 days of age (see Figure 10.16B). Similarly, in an experiment in which eggs of the flour beetle *Tribolium confusum* were placed in glass tubes (each with 0.5 g of food), death rates increased as the density of eggs per tube increased—again revealing density dependence (see Figure 10.16C). Density dependence has also been detected in populations whose abundance is strongly influenced by factors usually considered to act in a density-independent manner, such as temperature or precipitation; we describe one such example in **Web Extension 10.2**, in which Smith (1961) reanalyzed a classic example of density independence (Davidson and Andrewartha's thrips data).

When birth, death, or dispersal rates show strong density dependence, population growth rates (λ or r) may decline as densities increase (**Figure 10.17**). Eventually, if densities become high enough to cause λ to equal 1 (or r to equal 0), the population stops growing entirely; if λ becomes less than 1 (or $r < 0$), the population declines. As we'll see in the next section, such density-dependent changes in the population growth rate can cause a population to reach a stable, maximum population size.

CONCEPT 10.5

The logistic equation incorporates limits to growth and shows how a population may stabilize at a maximum size, the carrying capacity.

Logistic Growth

Some populations exhibit **logistic growth**, a pattern in which abundance increases rapidly at first and then stabilizes at a population size known as the **carrying capacity**, the maximum population size that can be supported indefinitely by the environment. The growth of such a population can be represented by an S-shaped curve (**Figure 10.18**). The growth rate of the population decreases as the population size nears the carrying capacity because resources such as food, water, or space begin to be in short supply. At the carrying capacity, the growth rate is zero, and hence the population size does not change.

The logistic equation models density-dependent population growth

To see how the idea of a carrying capacity can be represented in a mathematical model of population growth, let's reconsider Figure 10.17. The data in both graphs show that population growth rates (r or λ) decreased approximately as a straight line as population densities increased. But r is assumed to be constant in the exponential growth equation, $dN/dt = rN$. As we've seen, a constant value of $r > 0$ allows for unlimited growth in population size. Thus, to modify the exponential growth equation to make it more realistic, we replace the assumption that r is constant with the assumption that r declines in a straight line as density (N) increases. When we do

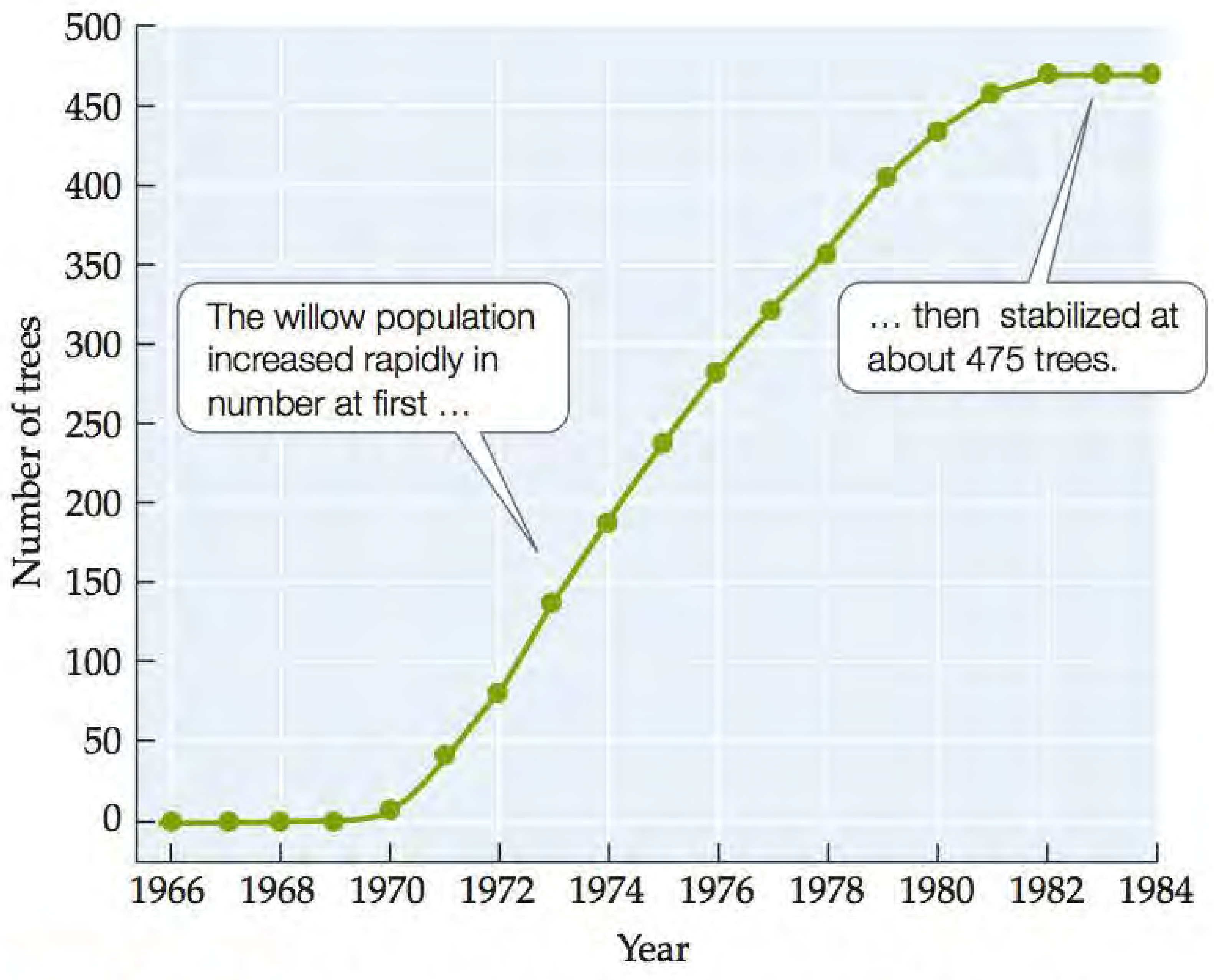


Figure 10.18 An S-Shaped Growth Curve in a Natural Population At a site in Australia, heavy grazing by rabbits had prevented willows from colonizing the area. The rabbits were removed in 1954, opening up new habitat for willows. When willows colonized the area in 1966, ecologists tracked the growth of their population. (After Alliende and Harper 1989.)

this, as described in **Web Extension 10.3**, we obtain the *logistic equation*:

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) \quad \textbf{(10.7)}$$

where dN/dt is the rate of change in population size at time t, N is population density (also at time t), r is the (per capita) intrinsic rate of increase under ideal conditions, and K is the density at which the population stops increasing in size. K can be interpreted as the carrying capacity of the environment, and the term $(1 - N/K)$ can be viewed as representing the net effect of factors that reduce the population growth rate from the constant rate (r) seen in exponential growth.

Logistic growth is similar to, but slightly slower than, exponential growth when densities are low (**Figure 10.19**). This occurs because when N is small, the term $(1 - N/K)$ is close to 1, and hence a population that grows logistically grows at a rate close to r. As the population density increases, however, logistic and exponential growth differ greatly. In logistic growth, the rate at which the population changes in size (dN/dt) approaches zero as the population size nears the carrying capacity, K. As a result, over time, the population size approaches K gradually, eventually remaining constant with K individuals in the population.

In Concept 11.1, we'll discuss the extent to which the growth of natural populations can be described by the S-shaped curve that results from the logistic equation; here, we examine efforts to fit the logistic equation to U.S. census data.

Can logistic growth predict the carrying capacity of the U.S. population?

In a groundbreaking paper published in 1920, Pearl and Reed examined the fit of several different mathematical models to U.S. census data for the period 1790–1910. Several of the approaches they tested did a good job of matching the historical data, but none included limits to the eventual size of the U.S. population. To address this shortcoming, they derived the logistic equation, which, unknown to them, had been first described in 1838 by the Belgian mathematician P. F. Verhulst. Pearl and Reed argued that the logistic equation provided a sensible way to represent population growth because it included limits to growth. When they fit the census data to the logistic curve, they obtained an excellent match, from which they estimated that the U.S. population had a carrying capacity of $K = 197{,}274{,}000$ people.

The logistic curve estimated by Pearl and Reed provides a good fit to U.S. population data through 1950. After that time, however, the actual population size differed considerably from Pearl and Reed's projections (**Figure 10.20**). By 1967, the carrying capacity (197 million) they had predicted had been surpassed. Pearl and Reed intended their estimate of the carrying capacity to represent the number of people that could be supported in the United States in a self-sufficient manner. They recognized that if conditions changed—for example, if agricultural productivity increased or if more resources were imported from other countries—the population could increase beyond 197 million. These and other changes have occurred, leading some ecologists and demographers to shift their focus from the human carrying capacity to the area required

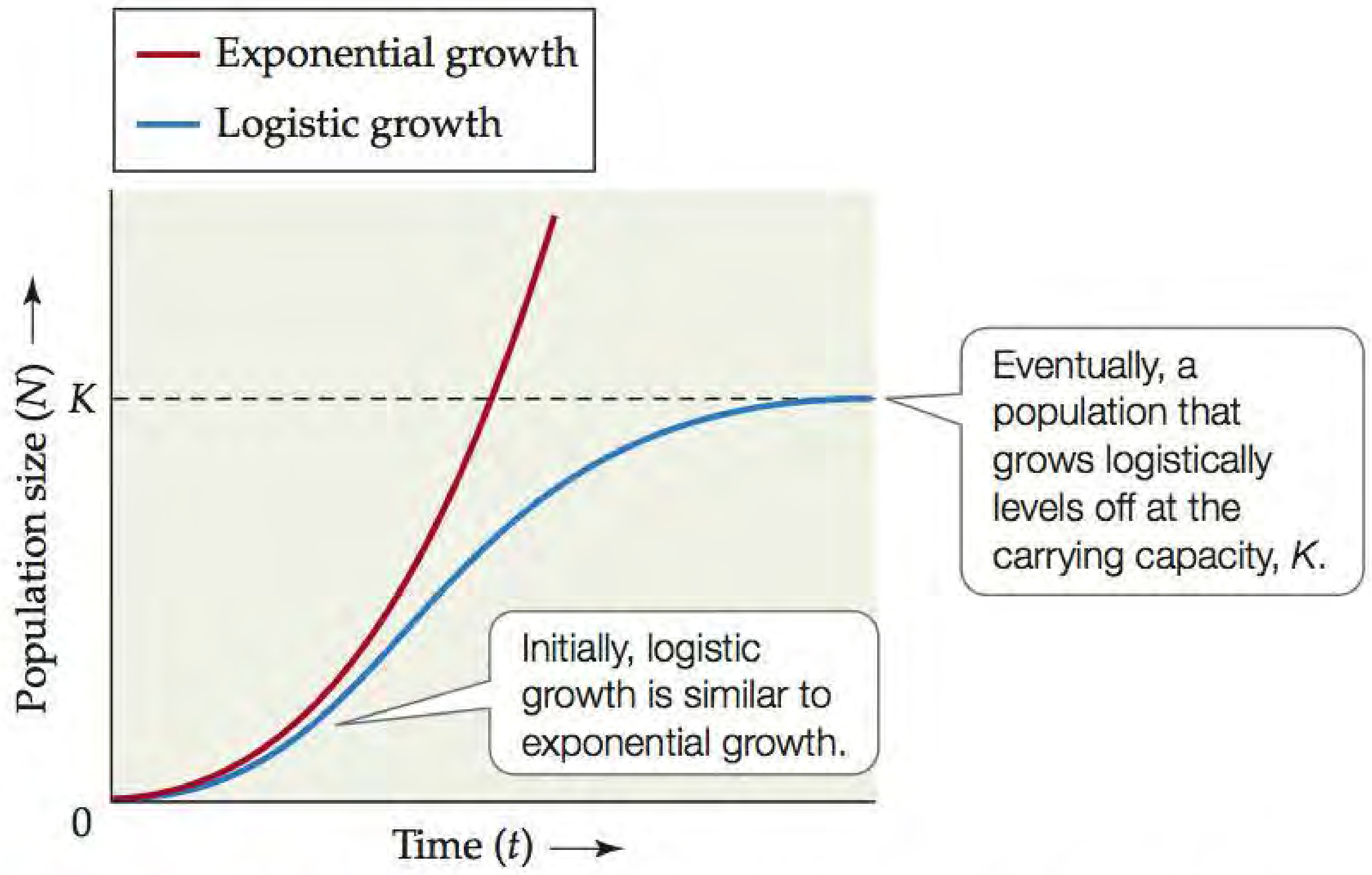


Figure 10.19 Logistic and Exponential Growth Compared Over time, logistic growth differs greatly from the unlimited growth of a population that increases exponentially.

? In the logistic equation, as the population size (N) becomes increasingly close to the carrying capacity, K, how does that affect the term $(1 - N/K)$? Why does this cause N to stop increasing in size?

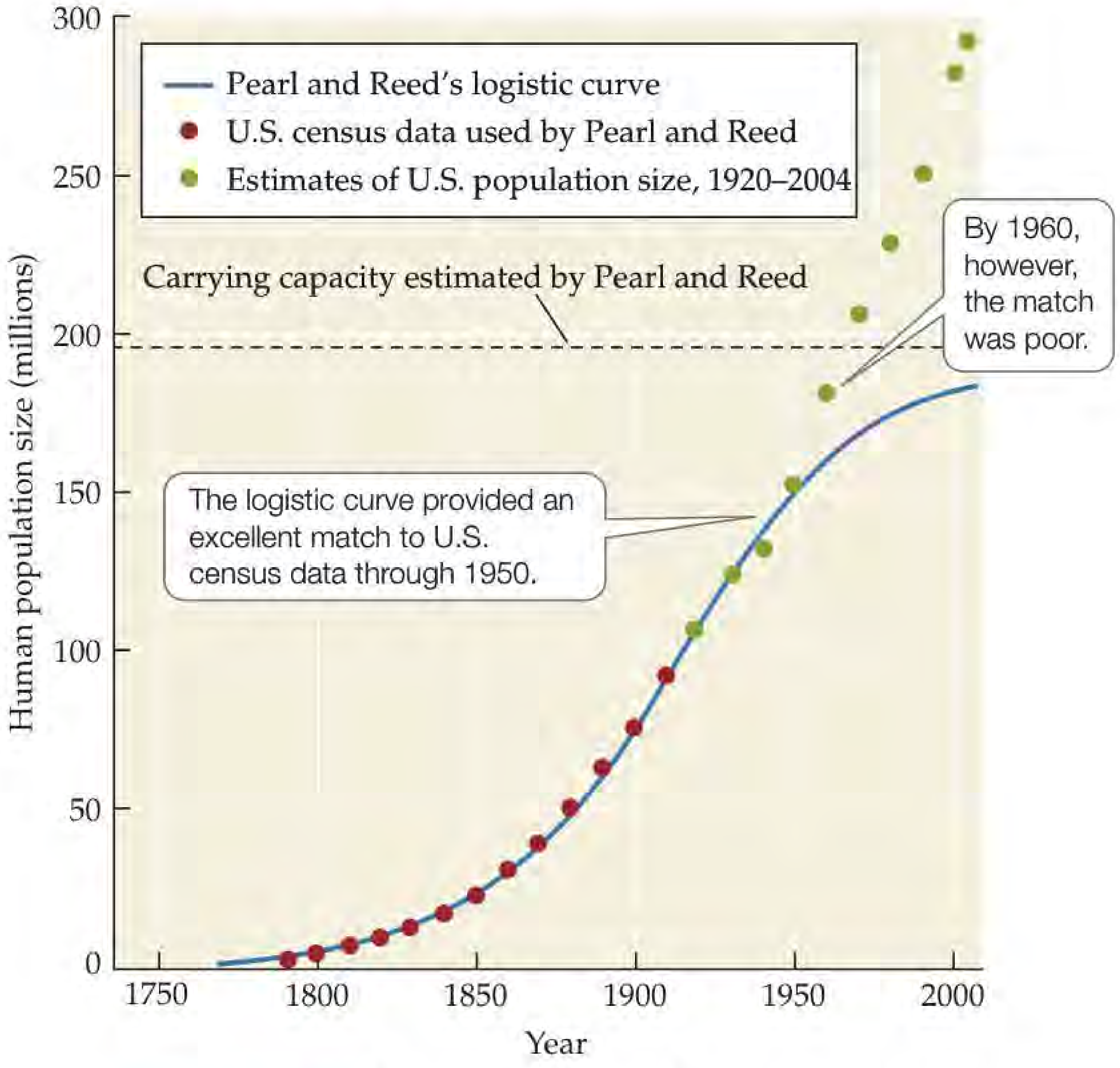


Figure 10.20 Fitting a Logistic Curve to the U.S. Population Size In 1920, Pearl and Reed fitted a logistic curve to U.S. census data for 1790–1910. They estimated the nation's carrying capacity (K) as 197 million people. (Data through 1910 from Pearl and Reed 1920; other data from Statistical Abstracts, U.S. Census Bureau.)

to support a human population (the "ecological footprint," discussed in Connections in Nature).

A CASE STUDY REVISITED

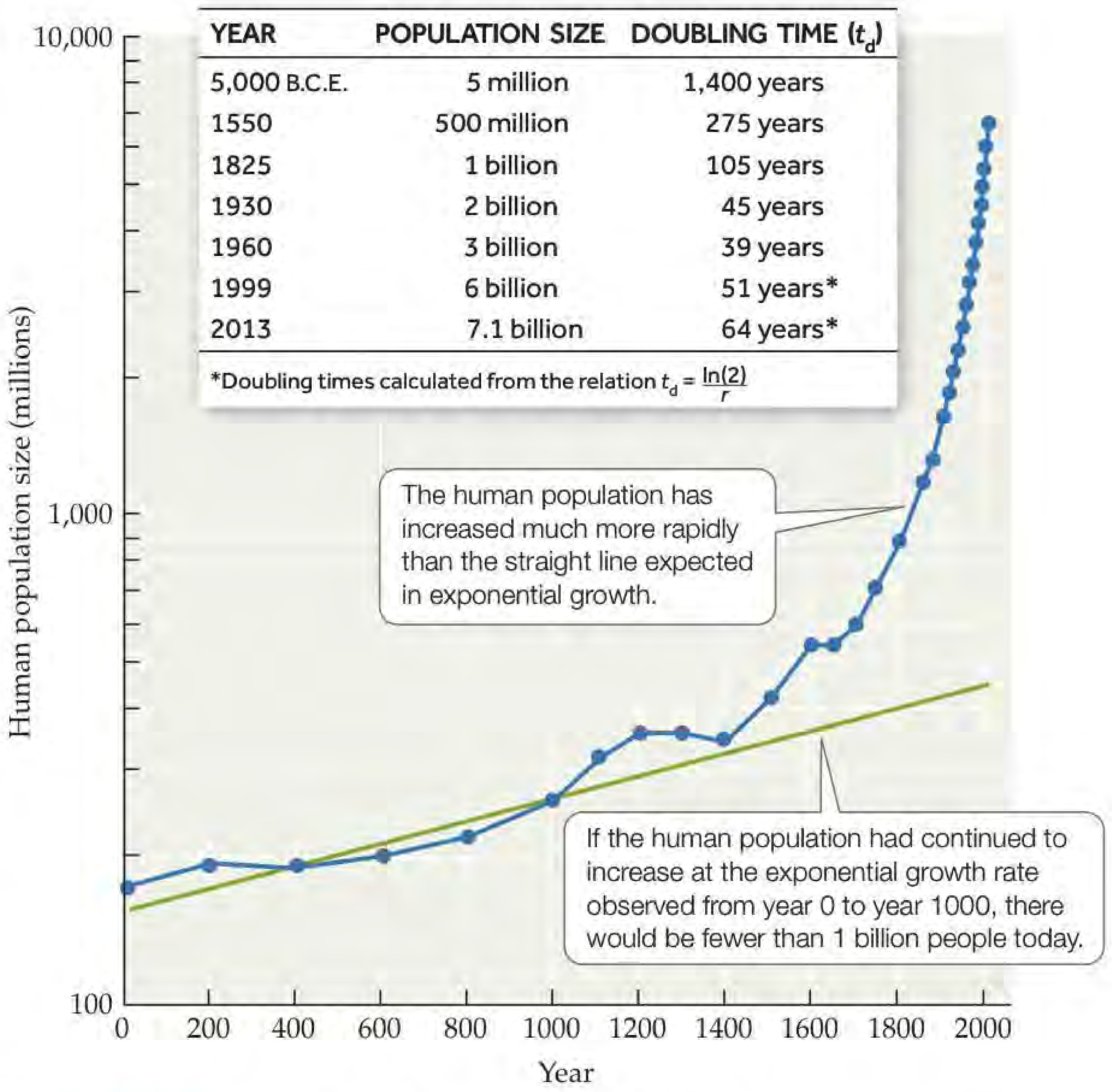
Human Population Growth

Media reports often state that the human population is growing exponentially. As we saw in Figure 10.11, a simple way to determine whether a population is growing exponentially is to plot the natural logarithm of population size versus time. If a straight line results, the population is growing exponentially. When we plot the natural logarithm of human population size versus time for the last 2,000 years, however, we see that our population sizes deviate considerably from the straight line expected in exponential growth (**Figure 10.21**). In fact, as fast as exponential growth is, historically the human population has increased even more rapidly than that.

The faster-than-exponential nature of human population growth is also evident from historical doubling times for the human population. Recall that in a population that grows exponentially, the doubling time remains constant. However, as shown in the inset of Figure 10.21, the doubling times observed for the human population dropped from roughly 1,400 years in 5000 B.C.E to a mere 39 years in 1960—again indicating that historically, our population has increased more rapidly than expected of exponential growth.

Projecting into the future, we can predict how long it will take our population to double in size at current rates of growth. To do this, the doubling time is estimated from the relation $t_d = \ln(2)/r$ (see Equation 10.5), where r is the current growth rate of the human population. Such estimates have shown that the human population was growing most rapidly in the early 1960s, with a doubling time of 32 years. Since then, the doubling time has increased (because r has decreased), reaching 64 years in 2013.

The increase in the doubling time (and the decrease in r) over the past 5 decades indicates that the human population is now growing more slowly than expected in exponential growth. So, returning to the question we asked in the Case Study (whether there would be 14 billion people in 2080), the answer is probably not. U.S. Census Bureau projections indicate that population growth rates are likely to continue to fall over the next 40 years (**Figure 10.22**), leading to a predicted population size of 9.6 billion in 2050 (**Figure 10.23**). Extending that curve out to 2080 suggests that there will be roughly 10 billion people in that year. If these projections turn out to be correct, or nearly so, what will the future be like with that



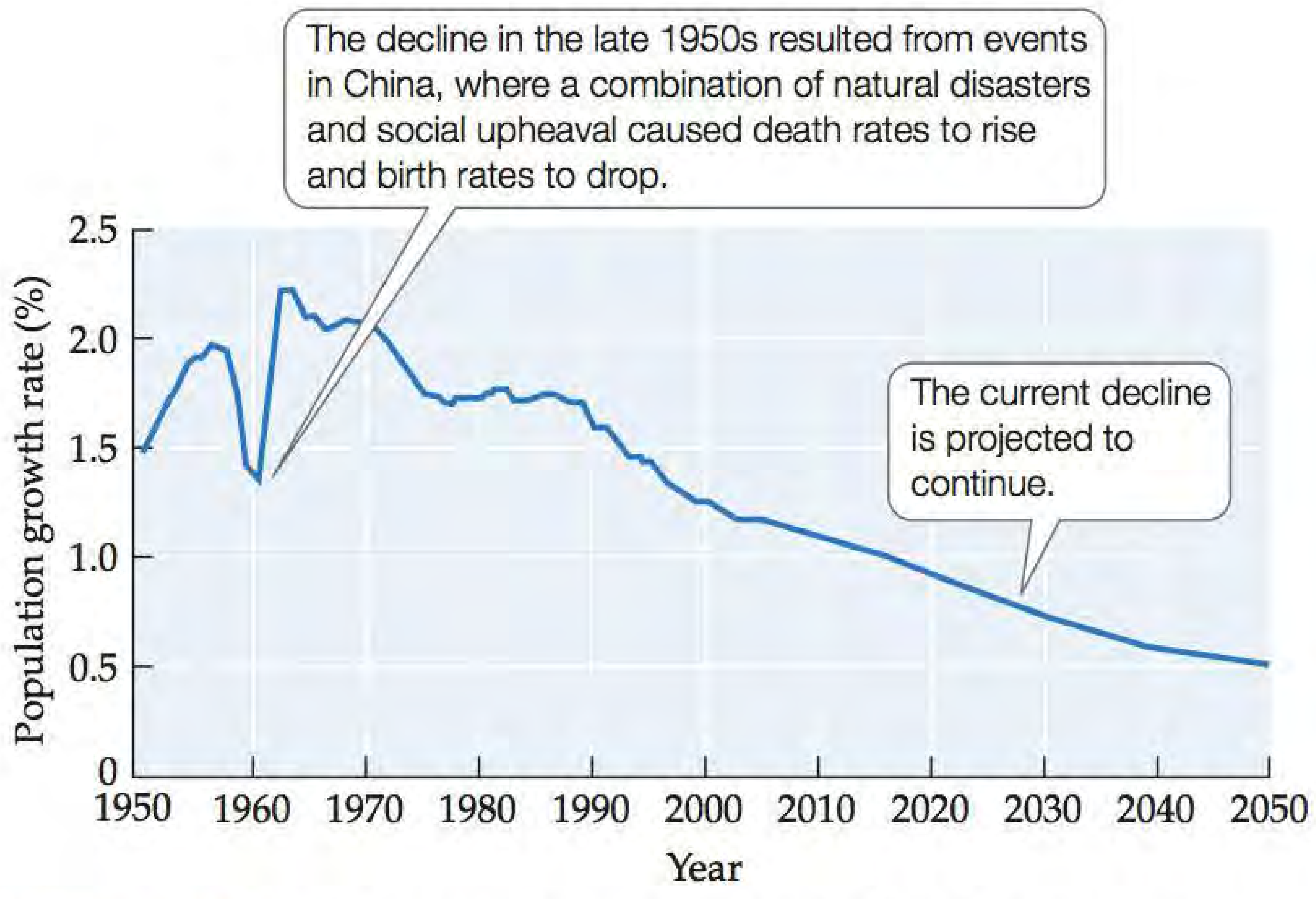
YEAR	POPULATION SIZE	DOUBLING TIME (t_d)
5,000 B.C.E.	5 million	1,400 years
1550	500 million	275 years
1825	1 billion	105 years
1930	2 billion	45 years
1960	3 billion	39 years
1999	6 billion	51 years*
2013	7.1 billion	64 years*

*Doubling times calculated from the relation $t_d = \frac{\ln(2)}{r}$

The human population has increased much more rapidly than the straight line expected in exponential growth.

If the human population had continued to increase at the exponential growth rate observed from year 0 to year 1000, there would be fewer than 1 billion people today.

Figure 10.21 Faster than Exponential A plot of the logarithm of the human population size over the last 2,000 years differs dramatically from the straight line expected if it were growing exponentially.



The decline in the late 1950s resulted from events in China, where a combination of natural disasters and social upheaval caused death rates to rise and birth rates to drop.

The current decline is projected to continue.

Figure 10.22 **World Population Growth Rates Are Dropping** Annual world population growth rates have declined since the early 1960s. (Data from U. S. Census Bureau, International Data Base, June 2011 update.)

? In 2050, will the human population still be increasing in size? Explain.

many people? Is 10 billion above the carrying capacity of the human population?

To answer these questions, we must determine the carrying capacity of the human population, but that is trickier than it may at first appear. Many researchers have estimated the human carrying capacity, obtaining values that range from fewer than 1 billion to more than 1,000 billion (see Cohen 1995). This large variation is due in part to the fact that many different methods—from logistic models to calculations based on crop production and human energy requirements—have been used. In addition, different researchers have made different assumptions about how people would live and how technology would influence our future, assumptions that have a large effect on the estimated carrying capacity.

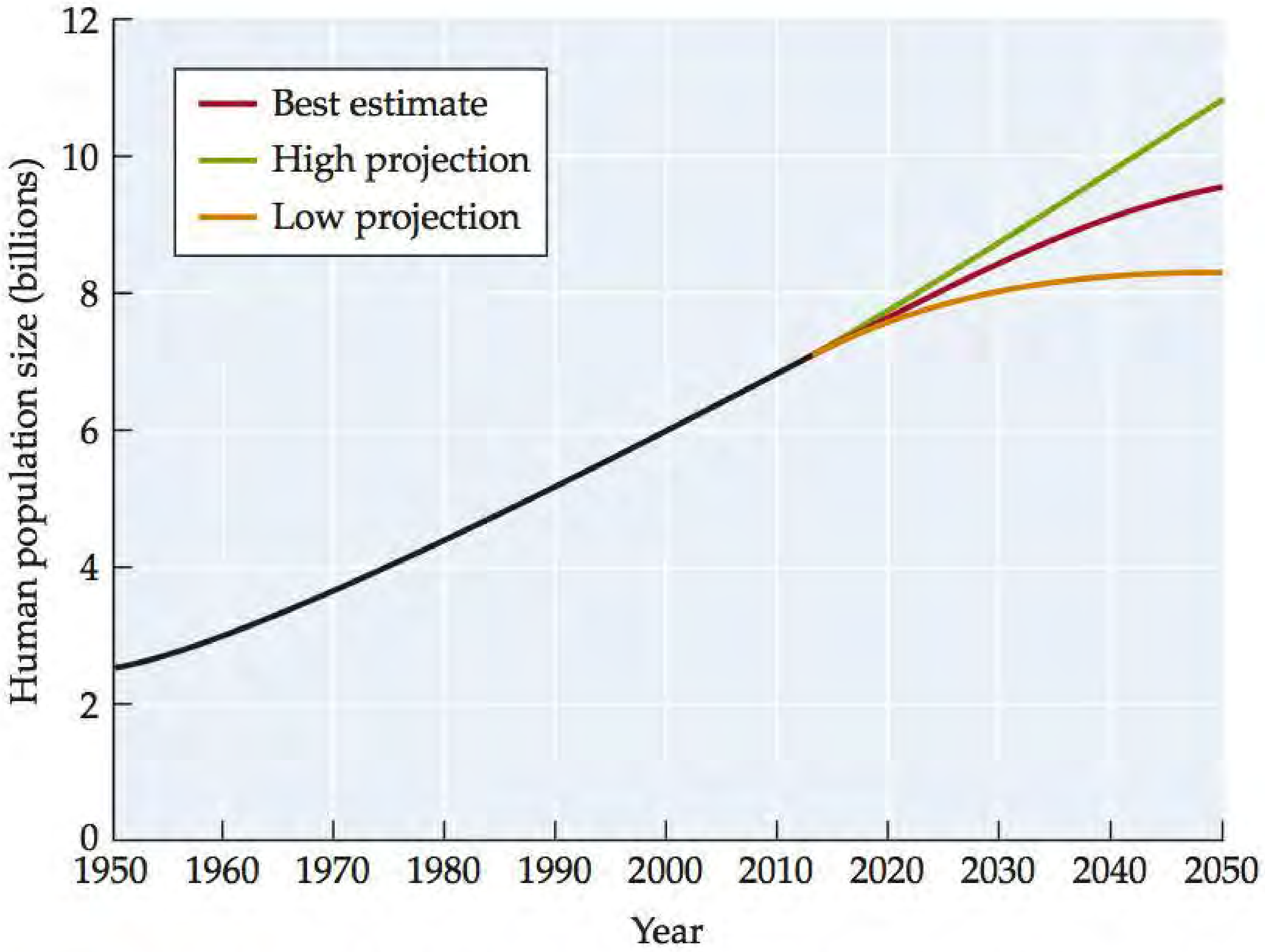


Figure 10.23 **United Nations Projections of Human Population Size** The human population is expected to increase to 9.6 billion by 2050; low and high projections range from 8.3 billion to 10.9 billion. (Data from United Nations, Department of Economic and Social Affairs, Population Division 2013.)

? Using the best-estimate curve shown here and the annual growth rate estimated for the human population in 2050 (see Figure 10.22), approximately how large will our population be in 2051?

For example, using the ecological footprint approach described in this chapter's Connections in Nature, it has been estimated that Earth could support 1.5 billion people indefinitely if everyone used the amount of resources used by people in the United States in 2007 (Ewing et al. 2010). On the other hand, if everyone used the amount of resources used by people in India in 2007, the world could support over 13 billion people. Thus, as we suggested in this chapter's Case Study, issues of human population size and resource use are linked inextricably: more people means that more resources will be used, but the degree to which our growing population affects the environment depends on the amount of resources used by each person.

CONNECTIONS IN NATURE
Your Ecological Footprint

When you turn on a light, purchase an appliance, drive a car, or eat fruit imported from another country, you may not think about the effects your actions have on the natural world. How, for example, does driving to the store to get groceries affect forests or coral reefs?

To answer this question, we must account for the resources required to support our actions. The grains we eat require farmland; the wood products we use require natural forests or plantations; the fish we eat require productive fishing grounds; the machines and appliances we purchase require raw materials and energy to build, as well as energy for their operation. Ultimately, every aspect of our economy depends on the land and waters of Earth. Recognizing this, William Rees proposed that we measure the environmental impact of a population as its **ecological footprint**, which is the total area of productive ecosystems required to support that population (Rees 1992). The ecological footprint approach turns the carrying capacity concept on its head: instead of asking how many people a given area can support, it asks how much area is required to support a given number of people.

Ecological footprints are calculated from national statistics on agricultural productivity, production of goods, and resource use. The area required to support these activities is then estimated. For example, the land required to support wheat consumption in 1993 by people in Italy was estimated by dividing the amount of wheat consumed (26,087,912 tons) by the amount of wheat produced per unit of land, which was 2.744 tons per hectare (ha). This resulted in 9,507,257 ha, or 0.167 ha per person (Wackernagel et al. 1999). To compare footprint calculations among nations and across different crops, such results are typically converted to *global hectares*, where a global hectare is defined as a hectare of world-average biological productivity (Kitzes and Wackernagel 2009).

Methods of calculating ecological footprints are still being refined, but results to date are sobering. In 2007, there were 11.9 billion global hectares of productive land available, and the ecological footprint of an average person was 2.7 global hectares (Ewing et al. 2010). These results suggest that Earth could have supported 4.4 billion people (11.9 billion ha/2.7 ha per person) for a long time. In fact, the human population in 2007 was 6.7 billion, more than a 50% overshoot of its carrying capacity. An overshoot of this magnitude indicates that in 2007, environmental resources were being used more rapidly than they could be regenerated, a pattern of use that cannot be sustained.

Similar calculations can be made for nations, cities, and even companies, schools, or individuals (see Review Question 4). In the United States, for example, the average ecological footprint was 8.0 global hectares per person in 2007. Since there were 1,330 million global hectares of productive land available in the nation, this calculation suggests that the carrying capacity of the United States in 2007 was 166 million people (1,330 million ha/8.0 ha per person); the actual population was 309 million, nearly double the carrying capacity.

Human use of resources changes from year to year, depending on population size, per capita rates of resource use, and technology (i.e., the efficiency of production). In addition, the total area of productive ecosystems available to support our activities changes over time because of factors such as gain or loss of farmland, destruction of natural habitat, pollution, and extinctions of species. As a result, our ecological footprint changes over time. People have now begun to use our changing footprint as a way to assess whether our current population size and resource use can be sustained. This approach highlights the fact that all of our actions—what we eat, how big a house we buy, how much we drive or fly, the goods we purchase (e.g., clothes, cars, cell phones)—depend on and affect the natural world.

Summary

CONCEPT 10.1 Life tables show how survival and reproductive rates vary with age, size, or life cycle stage.

- Cohort life tables can be constructed from data on the fates of individuals born during the same time period and used to calculate age-specific survival rate, survivorship, and fecundity.
- In highly mobile or long-lived organisms, a static life table may be constructed from data on the survival and fecundity of individuals of different ages during a single time period.
- In species for which age correlates poorly with survival and fecundity, life tables based on size or life cycle stage may be constructed.
- In a population with a type I survivorship curve, most individuals survive to old age. In a population with a type II survivorship curve, individuals experience a constant chance of surviving from one age to the next throughout their lives. In a population with a type III survivorship curve—the most common type in nature—death rates are very high for young individuals, but adults survive well later in life.

CONCEPT 10.2 Life table data can be used to project the future age structure, size, and growth rate of a population.

- The age structure of a population can affect the growth rate of that population over time.
- A population eventually grows at a fixed rate if age-specific survival rates and fecundities do not change over time.
- Any factor that changes age-specific survival rates or fecundities may alter a population's growth rate.

CONCEPT 10.3 Populations can grow exponentially when conditions are favorable, but exponential growth cannot continue indefinitely.

- Geometric growth occurs when a population of individuals that reproduce in synchrony at discrete time periods changes in size by a constant proportion from one discrete time period to the next.
- Exponential growth occurs when a population with continuous reproduction changes in size by a constant proportion at each instant in time.

Summary (Continued)

- Populations have the potential to increase rapidly in size because they grow by multiplication, not by addition.
- All populations experience limits to growth, which ensure that exponential growth cannot continue indefinitely.

CONCEPT 10.4 Population size can be determined by density-dependent and density-independent factors.

- In many species, density-independent factors, such as temperature or precipitation, play a major role in determining year-to-year changes in population size.
- When the density of any species becomes high enough, a lack of food, space, or other resources causes birth rates to decrease, death rates to increase, or dispersal to increase.
- Population regulation occurs when one or more density-dependent factors tend to increase population size when densities are low and decrease population size when densities are high.

CONCEPT 10.5 The logistic equation incorporates limits to growth and shows how a population may stabilize at a maximum size, the carrying capacity.

- In some species, changes in population size over time can be described by an S-shaped curve in which the population increases rapidly at first, then stabilizes at a maximum level, the carrying capacity.
- The logistic equation can be used to represent density-dependent population growth.
- Logistic population growth provides a close fit to the size of the U.S. population up to 1950; since that time, the growth rate of the U.S. population has been greater than expected in logistic growth.

CASE STUDY/CASE STUDY REVISITED Human population growth

- Over the past 2,000 years, the global human population has increased in size even more rapidly than it would if it were growing exponentially.
- Although the human population is still increasing rapidly in size, since the mid-1960s our population has grown more slowly than expected in exponential growth.
- Estimates of the carrying capacity of the human population vary widely, from fewer than 1 billion people to more than 1,000 billion people.
- The carrying capacity concept applies poorly to human populations that import resources from outside the area in which the population is found.
- Ecological footprint analyses based on available productive land area and current patterns of resource use suggest that the global human population is more than 50% greater than the maximum number that could be sustained for a long time.

Review Questions

1. For a field ecology project, you count the number of individuals of different ages found in a population during a single time period. There are 100 newborns, 40 1-year-olds, 15 2-year-olds, 5 3-year-olds, and 0 4-year-olds.
   - **a.** Use these data to fill in the N_x, S_x, and l_x columns of a static life table.
   - **b.** Explain the difference between a static life table and a cohort life table.
2. A population of insects triples every year. Initially, there were 40 insects.
   - **a.** How many insects will there be after 4 years?
   - **b.** How many insects will there be after 27 years? (Write your answer to this question as an equation.)
   - **c.** The habitat of the insect is degraded such that the population growth rate (λ) changes from 3.0 to 0.75. If there were 100 insects in the population when its habitat became degraded, how many insects will there be after 3 years?
3. What is the distinction between factors that regulate population size and factors that determine population size?
4. Calculate your ecological footprint at www.footprintnetwork.org/en/index.php/GFN/page/calculator

Hone Your Problem-Solving Skills

As discussed in this chapter, life table data can be used to estimate a population's growth rate (λ) and stable age distribution. Here we'll examine how the initial age distribution of a population affects its growth rate (λ) and stable age distribution. We'll consider two populations that grow according to the following life table:

AGE (x)	S_x	l_x	F_x
0	0.33	1.0	0
1	0.50	0.333	3
2	0	0.167	2
3		0	0

1. The first population initially has 50 newborns, 50 1-year-olds, and 50 2-year-olds (i.e., at time 0, $N_0 = 50$, $N_1 = 50$, and $N_2 = 50$). Use the life table above and the method in Table 10.4 to calculate how the age distribution changes from time $t = 0$ to time $t = 6$. What is your best estimate of the growth rate (λ) and stable age distribution of this population?
2. A second population grows according to this same life table but has a different initial age distribution: $N_0 = 80$, $N_1 = 50$, $N_2 = 20$. Calculate how the age distribution changes from $t = 0$ to $t = 6$, and estimate the growth rate (λ) and stable age distribution of this population.
3. Compare your answers to questions 1 and 2. Without performing further calculations, estimate the growth rate (λ) and stable age distribution of a third population that also grows according to the life table but has an initial age distribution of $N_0 = 10$, $N_1 = 50$, $N_2 = 90$.

ON THE COMPANION WEBSITE

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The website includes companions to all of the Analyzing Data exercises, Online Quizzes, Flashcards, Suggested Readings, and more. In addition, the following resources are available for this chapter:

Hands-On Problem Solving

10.1 Braving the Wild Frontier: Population Dynamics in the Arctic Ground Squirrel

10.2 Millions of Babies, but Few Children: Life Tables for Barnacles

Web Extensions

10.1 Deriving the Geometric Growth Equations

10.2 Density Dependence in *Thrips imaginis*

10.3 Deriving the Logistic Equation

Online Climate Change Connection

10.1 Consequences of Climate Change for Western Forest Communities

Population Dynamics

11

A Sea in Trouble: A Case Study

In the 1980s, the comb jelly *Mnemiopsis leidyi* (**Figure 11.1**) was introduced into the Black Sea, most likely by the discharge of ballast water from cargo ships. The timing of this invasion could hardly have been worse. At that time, the Black Sea ecosystem was already in decline due to increased inputs of nutrients such as nitrogen from sewage, fertilizers, and industrial wastes (and, as we'll see in this chapter's Connections in Nature, overfishing may also have contributed to the ecosystem's decline). The increased supply of nutrients had devastating effects across the northern Black Sea, where the waters are shallow (less than 200 m deep) and prone to problems that stem from **eutrophication** (an increase in the nutrient content of an ecosystem). As nutrient concentrations increased in these shallow waters, phytoplankton abundance increased, water clarity decreased, oxygen concentrations dropped, and fish populations experienced massive die-offs. Nutrient concentrations in deeper portions of the Black Sea also rose, causing increased phytoplankton abundance, but not fish die-offs.

Such was the situation when *Mnemiopsis* arrived. This marine invertebrate species is a voracious predator of zooplankton, fish eggs, and young fish. Furthermore, *Mnemiopsis* continues to feed even when it is completely full, which causes it to regurgitate large quantities of prey stuck in balls of mucus. Small prey encased in mucus survive poorly. As a result, the negative effect of *Mnemiopsis* on its prey outstrips even its considerable ability to digest food.

Following its arrival in the Black Sea in the early 1980s, *Mnemiopsis* gradually increased in numbers. Then, in 1989, *Mnemiopsis* populations exploded (**Figure 11.2A**), reaching astonishing biomass levels (1.5–2.0 kg/m^2) throughout the sea. The total biomass of *Mnemiopsis* in the Black Sea was estimated at 800 million tons (live weight) in 1989—far greater than the world's entire annual commercial fish catch, which has never exceeded 95 million tons.

The enormous numbers of *Mnemiopsis* present in 1989, and again in 1990, compounded the effects of the Black Sea's ongoing problems. *Mnemiopsis* ate huge quantities of zooplankton, causing their populations to crash (**Figure 11.2B**). Zooplankton eat phytoplankton, so *Mnemiopsis* indirectly caused phytoplankton populations to increase even more than they already had because of nutrient enrichment (**Figure 11.2C**). Upon their deaths, the phytoplankton and *Mnemiopsis* provided food for bacterial decomposers. Bacteria use oxygen as they decompose dead organisms, so as bacterial activity increased, oxygen concentrations in the water decreased, harming some fish populations. In addition, by devouring the food supplies

KEY CONCEPTS

CONCEPT 11.1 Population growth patterns include exponential growth, logistic growth, fluctuations, and regular cycles.

CONCEPT 11.2 Delayed density dependence can cause populations to fluctuate in size.

CONCEPT 11.3 The risk of extinction increases greatly in small populations.

CONCEPT 11.4 In metapopulations, sets of spatially isolated populations are linked by dispersal.

Figure 11.1 A Potent Invader The comb jelly *Mnemiopsis leidyi* was introduced from the east coast of North America to the Black Sea, wreaking havoc in its new ecosystem upon its arrival.

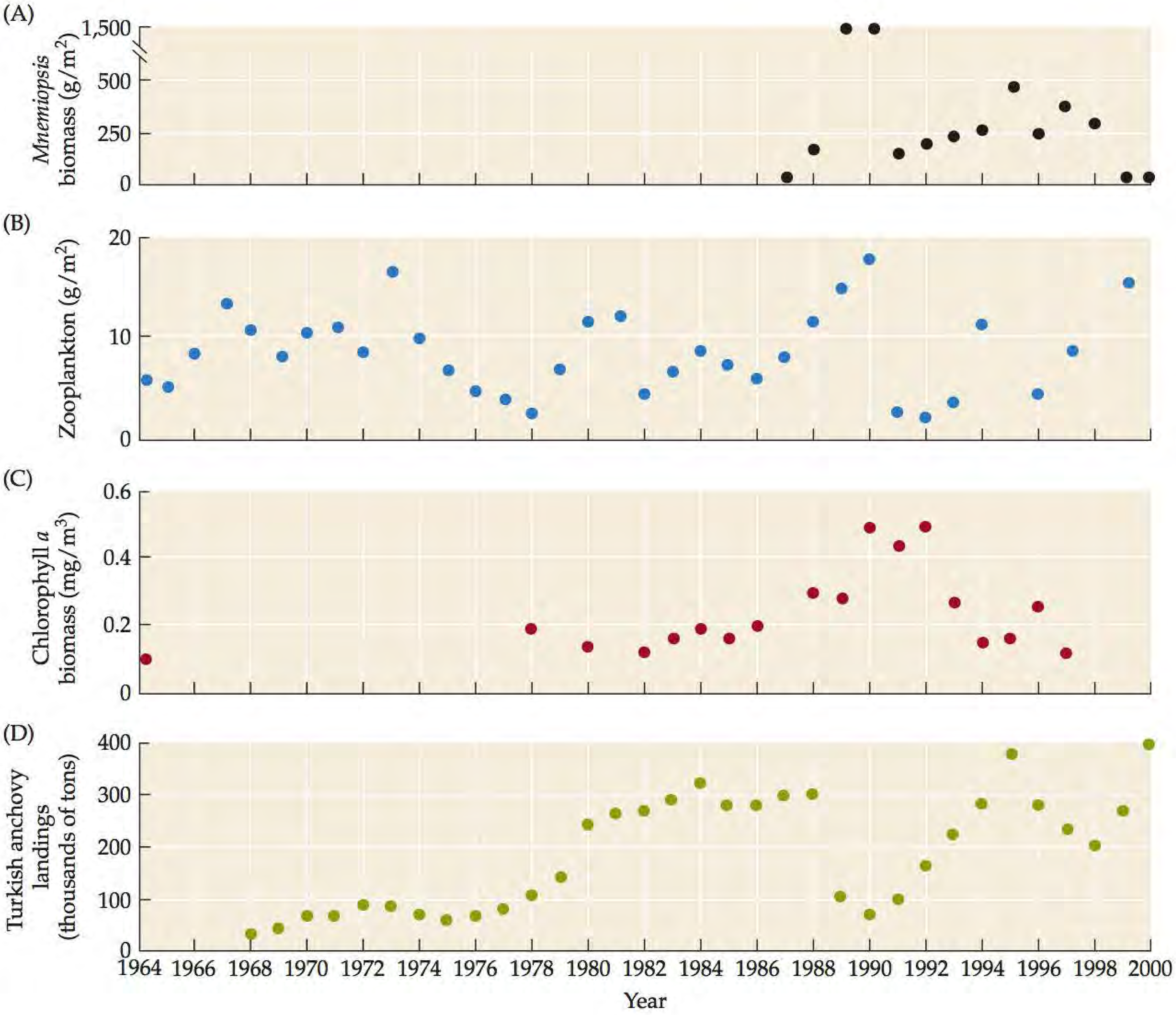


Figure 11.2 Changes in the Black Sea Ecosystem The graphs track long-term changes in four components of the Black Sea ecosystem: (A) mean biomass of the invasive species *Mnemiopsis leidyi* (first measured in 1987), (B) mean biomass of zooplankton, (C) mean biomass of chlorophyll *a* (an indicator of phytoplankton abundance), and (D) Turkish anchovy landings (Turkish fishermen have garnered most of the Black Sea anchovy catch since 1980). (After Kideys 2002.)

(zooplankton), eggs, and young of important commercial fishes such as anchovies, *Mnemiopsis* led to a rapid decline in fish catches (**Figure 11.2D**), causing extensive losses in the Turkish fishing industry.

The combined negative effects of nutrient enrichment and invasion by *Mnemiopsis* posed a serious threat to the Black Sea ecosystem. Although it covers a large surface area (over 423,000 km^2), the Black Sea is nearly landlocked and exchanges little of its water each year with other ocean waters. In addition, the Black Sea is unusual in that only the top 150–200 m of its waters (ca. 10% of its average depth) contain oxygen, which effectively makes the entire sea "shallow" for species that require oxygen. Its limited water exchange and anoxic deep waters make the Black Sea particularly vulnerable to the negative effects of nutrient enrichment.

Native Black Sea predators and parasites had failed to regulate *Mnemiopsis* populations. Thus, in the early 1990s, the future of the Black Sea ecosystem looked bleak. Fortunately, by the late 1990s, there were signs of improvement: *Mnemiopsis* and phytoplankton populations had fallen, paving the way for the recovery of the Black Sea. How did this happen?

Introduction

As we have seen in the previous two chapters, populations can change in size as a result of four processes: birth, death, immigration, and emigration. We can summarize the effects of these four processes on population size with the following equation:

$$N_{t+1} = N_t + B + I - D - E$$

where N_t is the population size at time t, B is the number of births, I is the number of immigrants, D is the number of deaths, and E is the number of emigrants between time t and time $t + 1$. As implied by this equation, populations are open and dynamic entities. Individuals can move from one population to another, and the number of individuals in a population can change from one time period to the next.

Ecologists use the term *population dynamics* to refer to the ways in which populations change in abundance over time. In this chapter, we'll consider the dynamics of populations in more detail, placing special emphasis on two kinds of populations: small populations that face the threat of extinction, and sets of populations that are linked by dispersal (metapopulations). We'll begin our discussion of population dynamics by surveying patterns of population growth.

CONCEPT 11.1

Population growth patterns include exponential growth, logistic growth, fluctuations, and regular cycles.

Patterns of Population Growth

Most observed patterns of population growth can be grouped into four major types: exponential growth, logistic growth, population fluctuations, and regular population cycles (a special type of fluctuation). Bear in mind, however, that a single population could experience each of these four types of growth at different times. Furthermore, these four patterns are not mutually exclusive. For example, as we will see shortly, a population may grow logistically yet fluctuate around the values expected in logistic growth.

Exponential growth can occur when conditions are favorable

In the first pattern, exponential growth, a population increases (or decreases) by a constant proportion at each point in time. As we saw in Concept 10.3, exponential growth can be represented by either of two related equations, $N_{t+1} = \lambda N_t$, for organisms that reproduce in synchrony at discrete time periods, or $dN/dt = rN$, for organisms that reproduce "continuously" (i.e., they reproduce at varying times that are not in synchrony).

Exponential growth cannot continue indefinitely, but when conditions are favorable, a population can increase exponentially for a limited time. Such periods of exponential growth can occur within the established range of a species, as when good weather occurs for several years running. They can also occur when a species reaches a new geographic area, either by dispersing on its own or with human assistance. If conditions are favorable in the new environment, the population can increase rapidly until density-dependent factors act to regulate its numbers (see Concept 10.4).

An example of how dispersal can lead to exponential growth is provided by the cattle egret subspecies *Bubulcus ibis ibis* (**Figure 11.3**). These birds originally lived in the Mediterranean region and in parts of central and southern Africa. Since the late 1800s and early 1900s, however, they have colonized new regions on their own, including South America and North America. Typically, after the subspecies reached a new area, its population in that area increased exponentially as it became established in its new habitat. For example, after the cattle egret colonized Florida in the 1950s, its populations there grew exponentially for several decades, with an estimated intrinsic rate of increase of $r = 0.11$ for the period 1956–1971 (van den Bosch et al. 1992). By the 1980s, exponential growth had ceased and cattle egret numbers in Florida had stabilized.

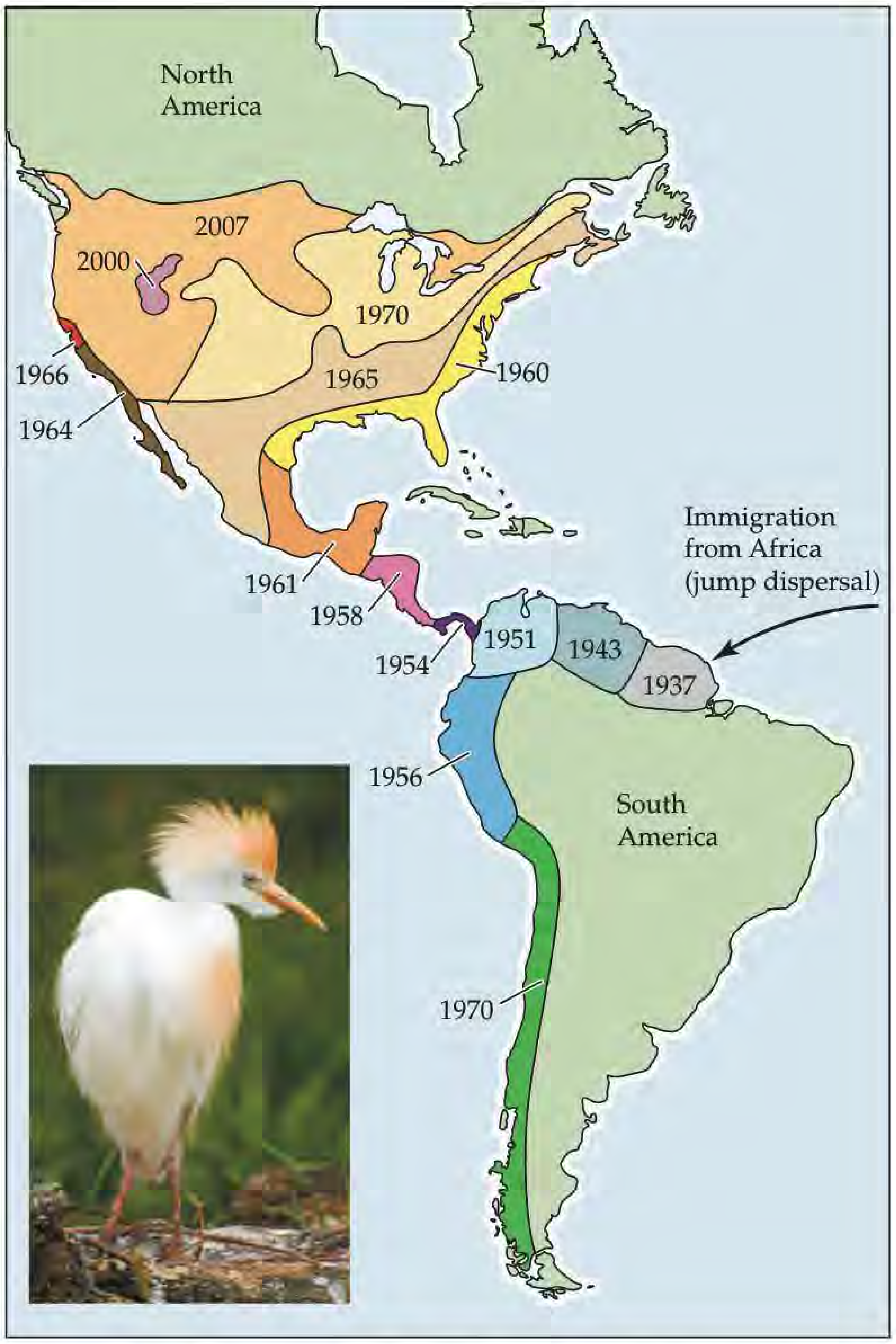


Figure 11.3 Colonizing the New World The cattle egret subspecies *Bubulcus ibis ibis* dispersed from Africa to South America in the late 1800s. Once it established colonies in the northeastern region of South America, it then spread rapidly to other parts of South and North America. The contour lines and dates show the edges of the cattle egret's range at different times. (After Osborn 2007.)

As in cattle egrets, species that successfully colonize new geographic regions on their own do so by long-distance or **jump dispersal** events. Local populations in the new region then increase in size—often growing exponentially—while also expanding (by relatively short-distance dispersal events) to occupy nearby areas of suitable habitat.

In logistic growth, the population approaches an equilibrium

Some populations appear to reach a relatively stable population size, or *equilibrium*, that changes little over time. When this occurs, the number of individuals first increases in size, then fluctuates by a relatively small amount around what appears to be the maximum sustainable population size. Such populations exhibit the second pattern of population growth, logistic growth (see Concept 10.5).

With few exceptions (see Figure 10.18), population growth does not match the predictions of logistic growth precisely. For example, the graph of sheep abundance in Tasmania over time (**Figure 11.4**) is only roughly similar to the characteristic S shape of a logistic curve. As this example suggests, when applied to natural populations, the term "logistic growth" is used broadly to indicate any population whose numbers increase initially but then level off and fluctuate around a maximum population size, the *carrying capacity*.

This lack of a perfect match is not surprising, given that in the logistic equation, $dN/dt = rN(1 - N/K)$ (Equation 10.7), the carrying capacity, K, is assumed to be a constant. For K to be a constant, the birth and death rates that occur at any particular density must not change from one year to the next (**Figure 11.5A**), a condition that rarely holds in nature. A more realistic scenario is shown in **Figure 11.5B**. Here, at any particular density, the birth rate or the death rate may take on a range of values, reflecting the fact that environmental conditions change over time. As a result, K also changes over time. When such a situation occurs, we would expect the population size to fluctuate around an average value of K, as observed for sheep in Tasmania (see Figure 11.4).

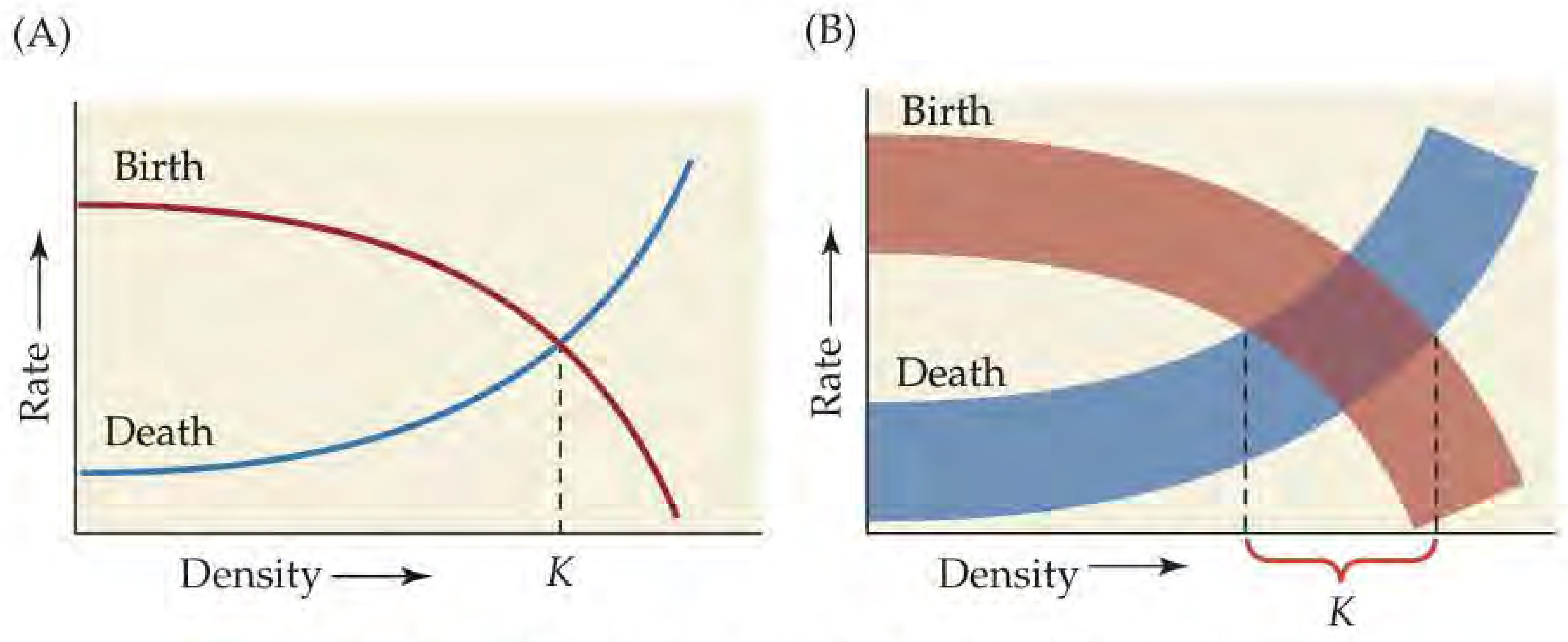


Figure 11.5 Why We Expect Carrying Capacity to Fluctuate The carrying capacity (K) of a population is the population size at which the birth rate equals the death rate. We can find K graphically by plotting the density at which the birth rate curve intersects the death rate curve. (A) Here we assume that at any given density, birth rates and death rates do not change over time. Hence, the two curves intersect at a single point, K, which is constant over time. (B) Here we assume that at any given density, both the birth rate and death rate vary over time, as indicated by the broad bands. As a result, the birth and death rate curves can intersect at a broad range of values, causing K to take on a range of values (shown in red) as well.

? In (A), draw a second death rate curve that is similar in shape to the curve in blue but has a higher death rate at each density. Label the carrying capacity that results, and compare it with the value of K shown in (A).

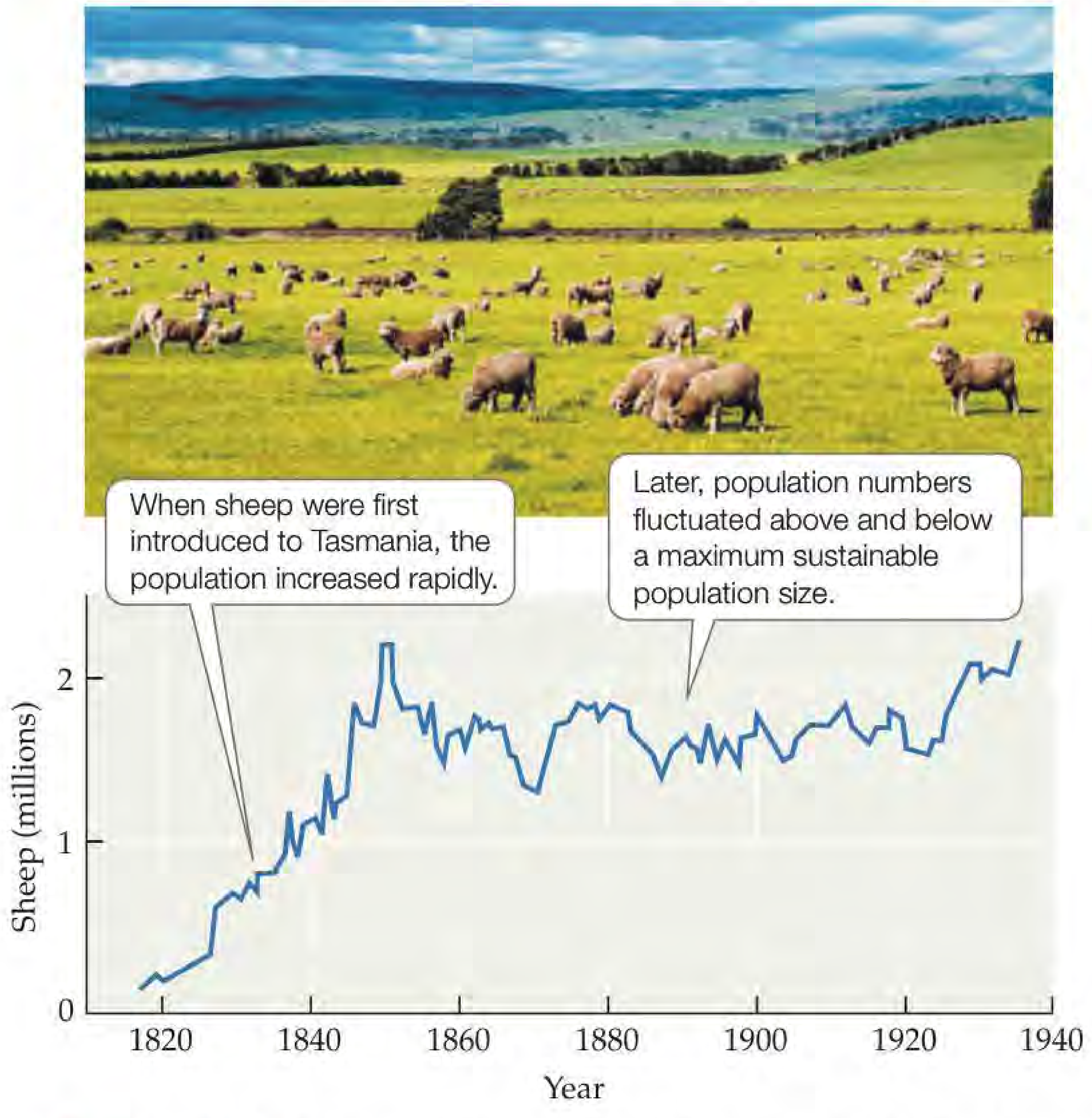


Figure 11.4 Population Growth Can Roughly Resemble a Logistic Curve Population growth in a few species matches a logistic curve closely (see Figure 10.18). More often, a species shows a pattern of growth (a rise in abundance, followed by a roughly stable population size) in which the match to a logistic curve is very rough, as seen here for sheep introduced to the island of Tasmania. (After Davidson 1938.)

All populations fluctuate in size

Another characteristic of the sheep population in Tasmania is seen in all populations: their size rises and falls over time, illustrating the third and most common pattern of population growth, **population fluctuations**. In some populations, fluctuations occur as erratic increases or decreases in abundance from an overall mean (**Figure 11.6**). In other populations, fluctuations occur as deviations from a population growth pattern, such as exponential or logistic growth. If, for example, the growth of a population exactly matched a logistic curve, the population would not be said to fluctuate. But if population abundances rose above and fell below those expected in logistic growth (as in the Tasmanian sheep), the population would be said to fluctuate.

In some cases, population fluctuations are relatively small (as seen in Figure 11.4). In other cases, the number of individuals in a population can explode at certain times, causing a population **outbreak** (**Figure 11.7**). As we saw in Figure 11.2A, the biomass of the comb jelly *Mnemiopsis*

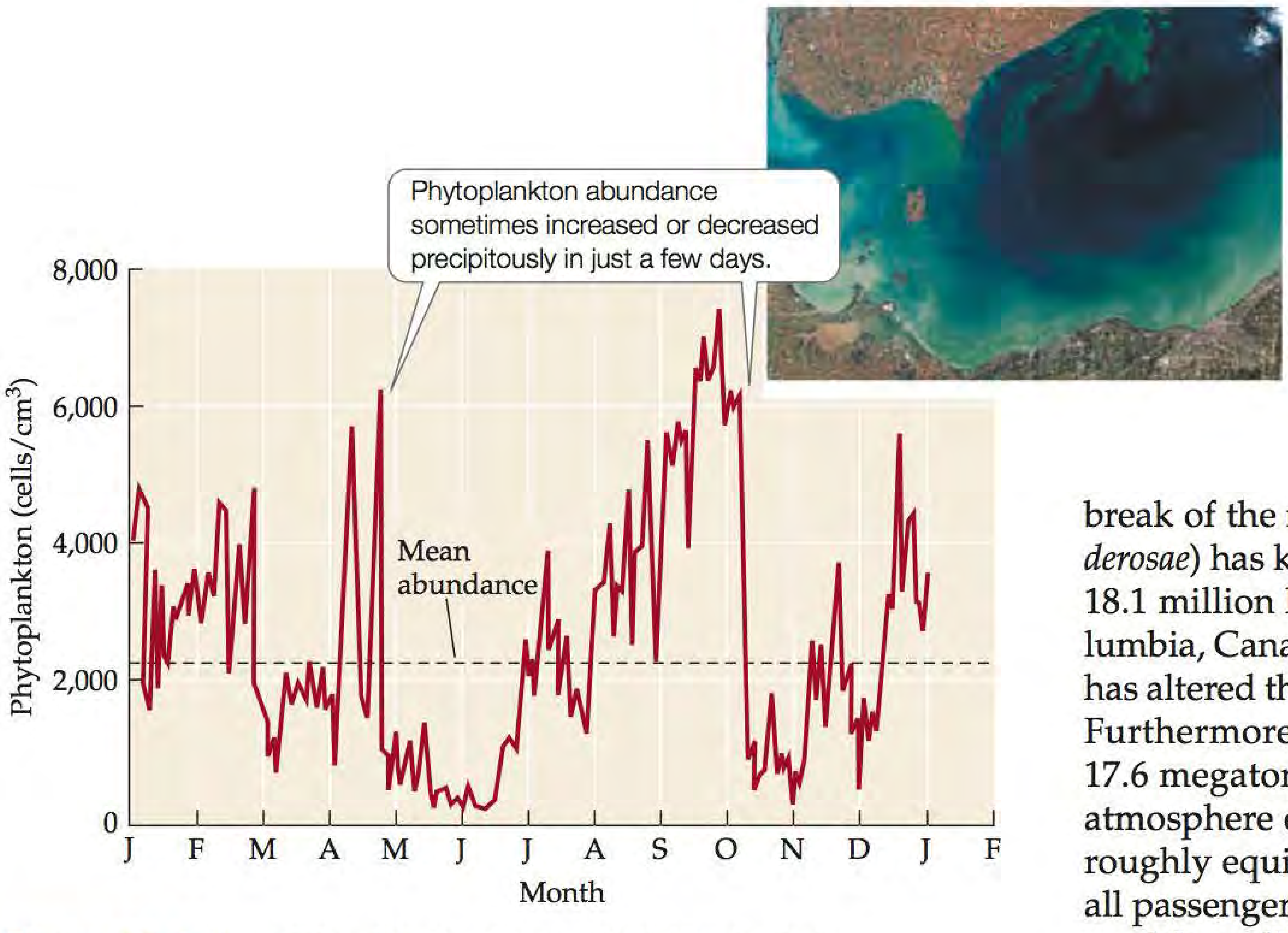


Figure 11.6 Population Fluctuations Variation in phytoplankton abundance in water samples taken from Lake Erie during 1962, showing fluctuations above and below the overall mean abundance of 2,250 cells per cubic centimeter. The inset shows an October 2011 phytoplankton "bloom" (a rapid increase in phytoplankton numbers) in the lake. (Graph after Davis 1964.)

increased 1,000-fold during a 2-year outbreak in the Black Sea. Rapid variations in population sizes over time have also been observed in many terrestrial systems, especially in insects. Census data for the bordered white moth (*Bupalus piniarius*) collected from 1882 to 1940 in a German pine forest showed that the densities reached during outbreaks were up to 30,000 times as great as the lowest density observed. Such outbreaks can have wide-ranging ecological effects. For example, since 2000, an ongoing outbreak of the mountain pine beetle (*Dendroctonus ponderosae*) has killed hundreds of millions of trees across 18.1 million hectares (45 million acres) in British Columbia, Canada (**Figure 11.8**). The death of these trees has altered the species composition of affected forests. Furthermore, as the dead trees decay, an estimated 17.6 megatons of carbon dioxide is released into the atmosphere each year (Kurz et al. 2008)—an amount roughly equivalent to the yearly carbon emissions of all passenger cars in Great Britain.

Many different factors, both density-independent and density-dependent, can cause the size of a population to fluctuate. The increase in zooplankton populations in the Black Sea in the early 1980s probably occurred because their prey (phytoplankton) had increased in abundance (see Figure 11.2). Then, in 1991, zooplankton numbers plummeted, probably because of the spectacular increase in the abundance of their predator (*Mnemiopsis*) during the previous 2 years. The rapid changes in phytoplankton abundance in Lake Erie shown in Figure 11.6 could reflect changes in a wide range of environmental factors, including nutrient supplies, temperature, and predator abundance. In some cases, such factors produce a striking type of fluctuation: population cycles.

Figure 11.7 Populations Can Explode in Numbers As we saw in Concept 10.3, all species have the potential for exponential growth. Hence, when conditions are favorable, a population outbreak can occur in which numbers increase very rapidly. The cockroaches covering the kitchen in this exhibit from the National Museum of Natural History represent the number that could have been produced by a single pregnant female in a few generations.

Figure 11.8 Consequences of an Insect Outbreak This aerial view shows the red foliage of lodgepole pine (*Pinus contorta*) trees killed by an outbreak of mountain pine beetles in British Columbia, Canada.

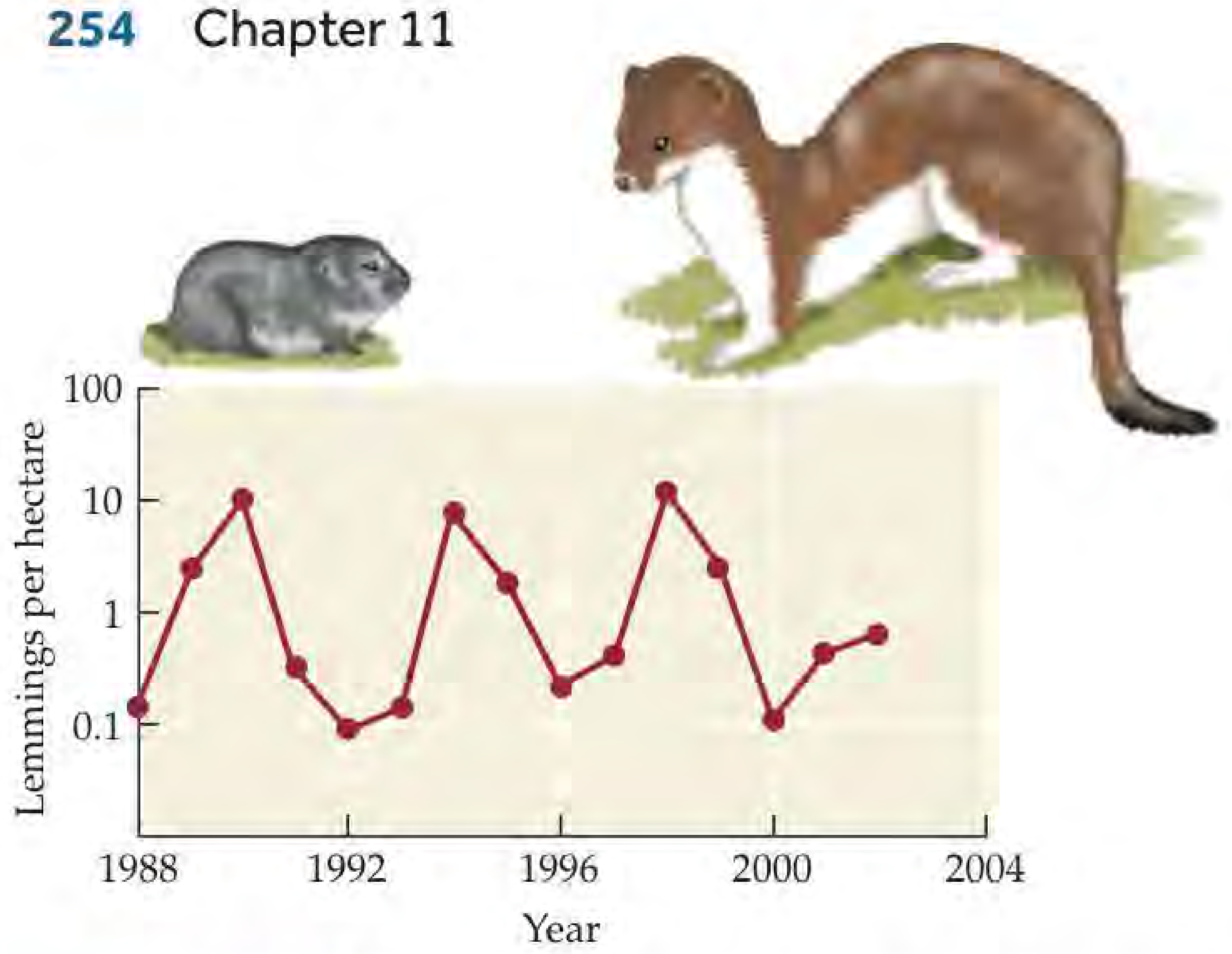


Figure 11.9 A Population Cycle In northern Greenland, collared lemming (*Dicrostonyx groenlandicus*, left) abundance tends to rise and fall every 4 years. In this location, the population cycle appears to be driven by predators, the most important of which is the stoat (*Mustela erminea*, right). In other regions, lemming population cycles may be driven by food supply. (After Gilg et al. 2003.)

? Based on data from 1988 through 2000, how many lemmings per hectare would you have expected there to be in 2002? Explain your reasoning.

Some species exhibit population cycles

The fourth pattern of population growth is **population cycles**, in which alternating periods of high and low abundance occur after constant (or nearly constant) intervals of time. Such regular cycles have been observed in populations of small rodents such as lemmings and voles, whose abundances typically reach a peak every 3–5 years (**Figure 11.9**).

Population cycles are among the most intriguing patterns observed in nature. After all, what factors can cause numbers to fluctuate greatly over time, yet maintain a high degree of regularity? Possible answers to this question include both internal factors, such as hormonal or behavioral changes in response to crowding, and external factors, such as weather, food supplies, or predators. Gilg et al. (2003) used a combination of field observations and mathematical models to argue that the 4-year cycle of collared lemming (*Dicrostonyx groenlandicus*) abundance in Greenland is driven by predators, one of which, the stoat, specializes on lemmings (see Figure 11.9). Other investigators have suggested that cycles of the Norwegian lemming (*Lemmus lemmus*) are caused by interactions between lemmings and their food plants. Similarly, a number of studies (e.g., Korpimäki and Norrdahl 1998) have implicated predators as the driving force behind cycles of field voles in Scandinavia, but Graham and Lambin (2002), in a large-scale field experiment, showed that predator removal had no effect on field vole cycles in England. As these conflicting results suggest, a universal cause of population cycles in small rodents has not emerged. Instead, ecological mechanisms that drive population cycles may differ from place to place and from one species to another—as is also true for factors that influence amphibian declines (see Figure 1.13).

CLIMATE CHANGE CONNECTION

Collapsing Population Cycles and Climate Change Recent evidence suggests that population cycles may stop entirely if key environmental conditions change. For example, population cycles of lemmings (including the cycle shown in Figure 11.9), voles, and several insect herbivores have decreased in amplitude or ceased entirely in some high-latitude and high-elevation locations (Gilg et al. 2009; Johnson et al. 2010; Cornulier et al. 2013).

What factors can cause the collapse of a population cycle? Some evidence points to climate change as a possible cause. Lemmings, for example, thrive when warmth from the ground melts a thin layer of the snow cover, leaving a small gap between the ground and the snow. In some regions, warmer winter temperatures have caused the snow to melt and refreeze, preventing the formation of these gaps. As discussed in Gilg et al. (2009), a shortage of gaps has made it more difficult for lemmings to feed and has made lemmings easier for their predators to catch. By holding lemming abundance in check (due to increased predation), these changes may have prevented lemming populations from increasing greatly in abundance every 3–4 years, thus halting the population cycles previously observed for this species (see Figure 11.9).

Climate warming also may have contributed to the collapse of vole population cycles throughout Europe and across different species (Cornulier et al. 2013). This hypothesis is reasonable since temperatures have increased and climate warming could affect populations of different species across Europe. However, vole cycles in some areas of Finland have continued despite regional warming, indicating that the effect of climate change may depend on the species or on the particular mechanisms that drive the cycles (Brommer et al. 2010). Moreover, the collapse of a population cycle can be caused by factors other than climate change. For example, Allstadt el al. 2013 concluded that the recent collapse of cycles in Canadian populations of the gypsy moth (*Lymantria dispar*) resulted from attack by a specialist pathogen rather than climate change. (See **Online Climate Change Connection 11.1** for further discussion of climate change and population cycles.).

CONCEPT 11.2

Delayed density dependence can cause populations to fluctuate in size.

Delayed Density Dependence

Although relatively few populations exhibit regular population cycles, all populations fluctuate in size to some degree. As we've seen, such fluctuations can result from a variety of factors, including changes in food supply, temperature, or predator abundance. Population fluctuations can also be caused by delayed density dependence, the effects of which we examine here.

The effect of population density is often delayed in time

Delays, or time lags, are an important feature of interactions in nature. For example, when a predator or parasite feeds, it does not produce offspring immediately; thus, there is a built-in delay in the effect of food supply on birth rates. As a result, it is common for the number of individuals born in a given time period to be influenced by the population densities or other conditions that were present several time periods ago.

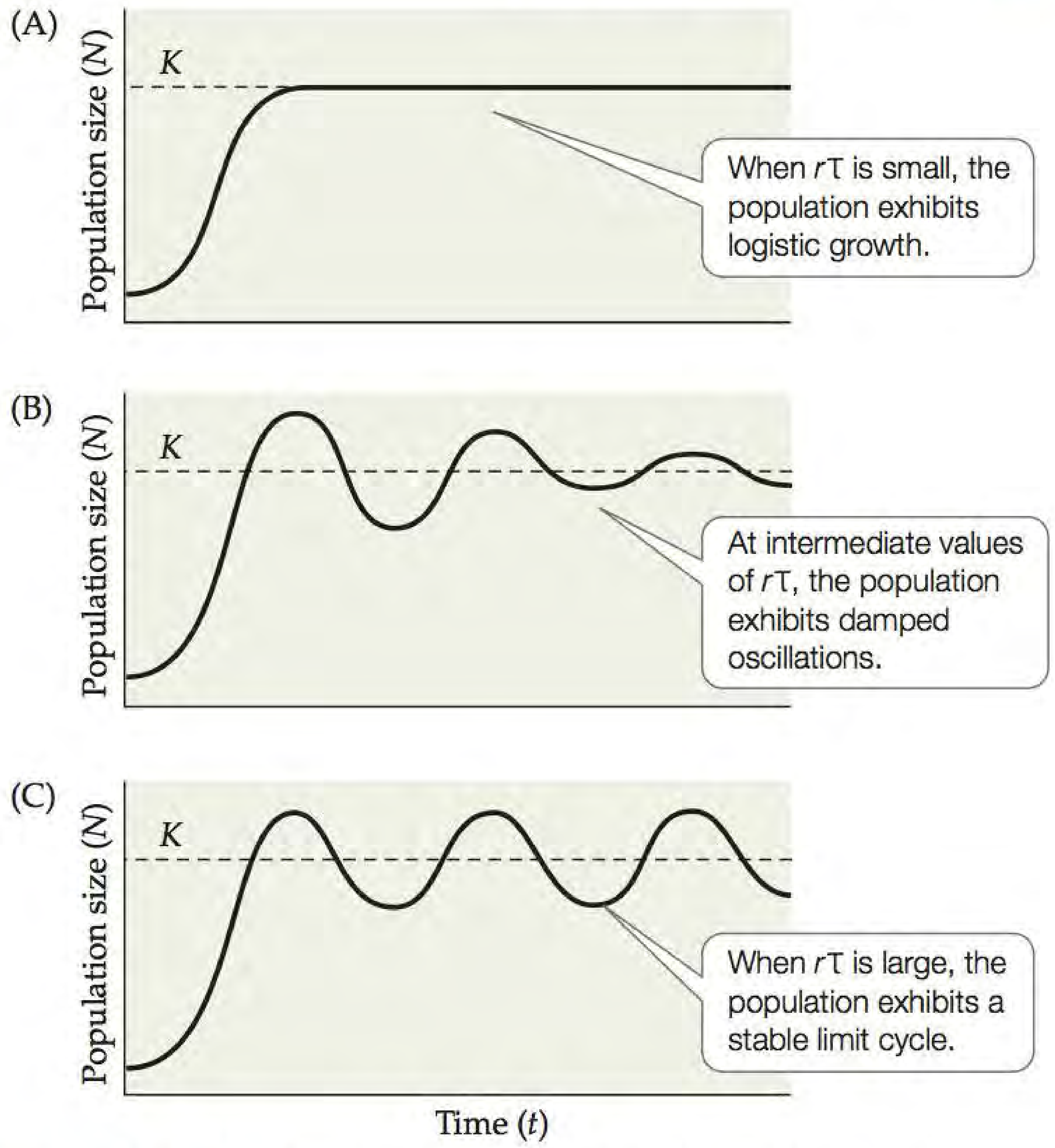
Beginning in the 1920s and 1930s, ecologists examined such time lags with mathematical models that incorporated **delayed density dependence** (delays in the effect that density has on population size). Results from these models indicated that delayed density dependence can contribute to population fluctuations.

Intuitively, this finding makes sense. Consider a population of predators that reproduce more slowly than their prey. If there are few predators initially, the prey population may increase rapidly in size. As a result, the predator population may also increase, reaching a point at which there are many adult predators that survive well and produce a large number of offspring. However, if the resulting large population of predators eats so many prey that the prey population decreases sharply in size, there may be few prey available for the next generation of predators. In such a case, a mismatch in predator and prey numbers (high predator numbers, low prey numbers) occurs because there is a time lag in the response of predator numbers to prey numbers. When such a mismatch takes place, the predators may survive or reproduce poorly and their numbers may drop. If prey numbers then increase (because there are now fewer predators), predator numbers may first rebound, then fall again because of the built-in time lag. Thus, in principle at least, it seems reasonable that a delay in the response of predators to prey density could cause predator numbers to fluctuate over time.

To examine further how delayed density dependence affects population fluctuations, consider the following version of the logistic equation, modified to include a time lag, τ:

$$\frac{dN}{dt} = rN\left[1 - \frac{N_{(t-\tau)}}{K}\right] \tag{11.1}$$

In this equation, dN/dt is the rate of change in population size at time t, r is the (per capita) intrinsic rate of increase under ideal conditions, N is the population size at time t, and K is the carrying capacity. Equation 11.1 is identical to the logistic equation (Equation 10.7), except that within the term $(1 - N/K)$, N has been replaced by $N_{(t-\tau)}$, the population size at time $t - \tau$. Recall that the term $(1 - N/K)$ represents the net effect of factors that reduce the (per capita) population growth rate from the constant rate (r) seen in exponential growth. Incorporating $N_{(t-\tau)}$ within this term indicates that the population growth rate is reduced by the size of the population at time $t - \tau$ in the past—not by the population's current size, $N_{(t)}$, as was assumed in Equation 10.7.



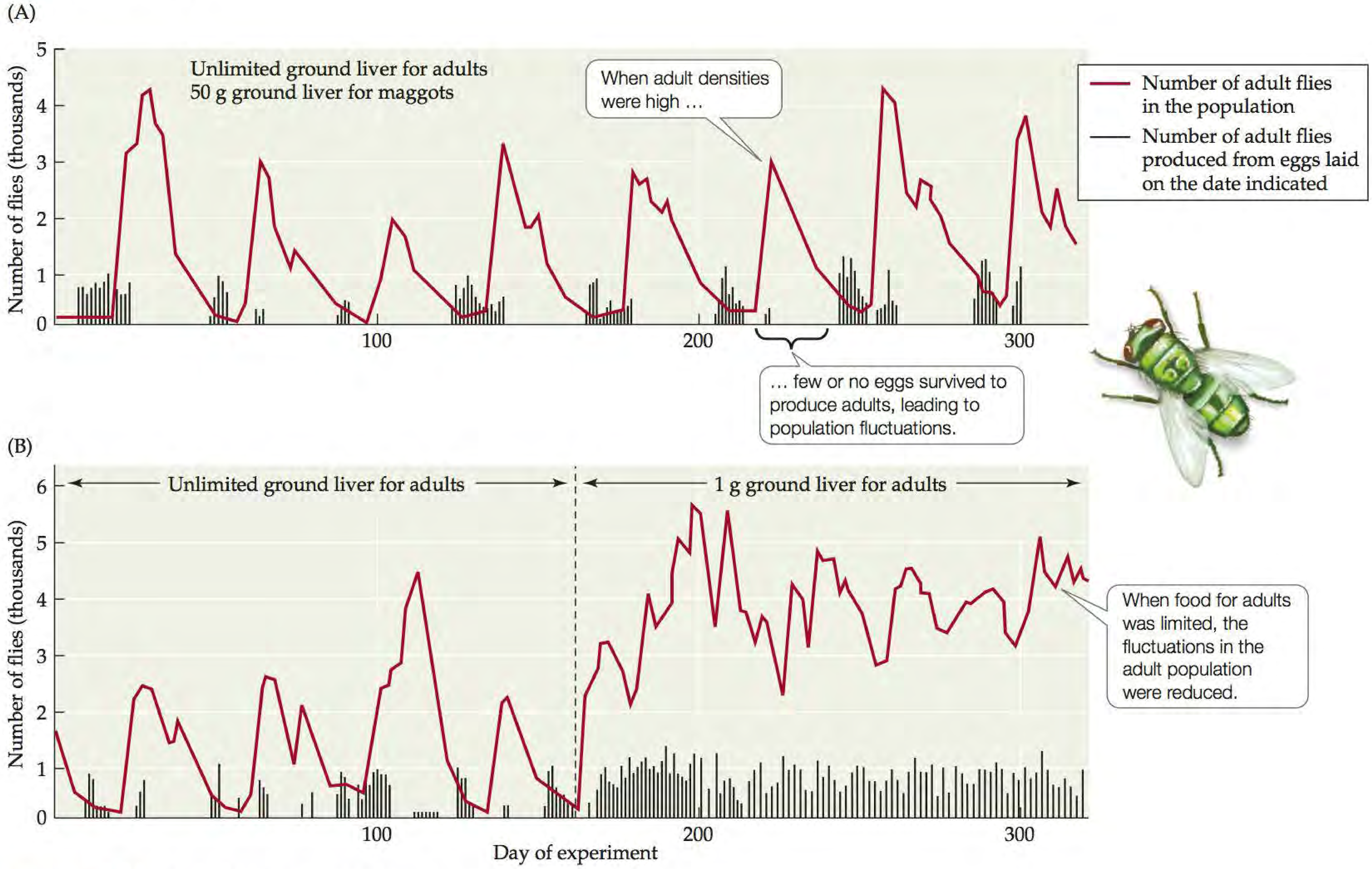
When $r\tau$ is small, the population exhibits logistic growth.

At intermediate values of $r\tau$, the population exhibits damped oscillations.

When $r\tau$ is large, the population exhibits a stable limit cycle.

Figure 11.10 Logistic Curves with Delayed Density Dependence Depending on the values of the intrinsic rate of increase (r) and the time lag (τ), adding delayed density dependence to the logistic equation can result in (A) an S-shaped logistic curve; (B) damped oscillations, a pattern of fluctuations around the carrying capacity, K, that become smaller over time; or (C) a stable limit cycle, a regular cycle of ongoing fluctuations around the carrying capacity.

When we incorporate delayed density dependence into the logistic equation in this way, population fluctuations can result (**Figure 11.10**). Robert May (1976) studied the behavior of Equation 11.1 and showed that the occurrence of such fluctuations depends on the values of the parameters r and τ. Specifically, he found that when the product of those parameters is "small" ($0 < r\tau < 0.368$), the population increases smoothly to the carrying capacity, K (see Figure 11.10A). At intermediate values of $r\tau$ ($0.368 < r\tau < 1.57$), delayed density dependence causes the population to fluctuate in size (see Figure 11.10B). The result is a pattern of **damped oscillations**, in which the deviations from the carrying capacity gradually get smaller over time. Finally, when $r\tau$ is "large" ($r\tau > 1.57$), the population exhibits a regular cycle in which it fluctuates indefinitely around the carrying capacity, K (see Figure 11.10C); such a pattern is called a **stable limit cycle**.



When adult densities were high …

… few or no eggs survived to produce adults, leading to population fluctuations.

When food for adults was limited, the fluctuations in the adult population were reduced.

Figure 11.11 Nicholson's Blowfly Experiments (A) Adult blowflies were supplied with unlimited food, maggots with limited food. As a result, few or no adults were produced from the many eggs laid during periods of maximum adult abundance, because the many maggots that hatched from those eggs had insufficient food to eat. (B) Experimental conditions were the same as in part (A) until roughly halfway through the experiment (indicated by the dotted vertical line), when the food supply for adults was also limited. (After Nicholson 1957.)

? Which of the four population growth patterns discussed under Concept 11.1 best characterizes the results shown in (A)? In (B)? Explain.

Overall, the results in Figure 11.10 indicate that population fluctuations become more pronounced as the product $r\tau$ increases. This observation makes intuitive sense: when a population grows very rapidly (large r), or when there is a very long time lag (large τ), the size of the population can become much larger than the carrying capacity before its numbers start to decline. We turn now to experiments designed to test the effects of delayed density dependence in laboratory populations.

Delayed density dependence produces cycles in blowfly populations

In the 1950s, A. J. Nicholson performed a series of pioneering laboratory experiments on density dependence in blowflies. These insects are both decomposers and parasites in that they feed on dead animals but also attack living hosts, including mammals and birds. Nicholson studied *Lucilia cuprina*—the sheep blowfly—so named because it is an important agricultural pest of sheep. Before they can lay eggs, the females of this species need a protein meal (which they usually get from animal dung or carcasses). Once they have fed, the females attack living sheep by laying their eggs near the tail or near open wounds or sores. Small white maggots hatch from those eggs and feed on dung attached to the skin or on exposed flesh. As they feed, the maggots grow larger and more voracious. At a certain point, the maggots burrow inside the sheep, where they feed on its internal tissues, causing severe lesions and sometimes death. Death can be caused directly by the maggots (as a result of their feeding activities) or by infections that spread through the lesions. The sheep blowfly's full life cycle (from egg to egg) can be completed in as little as 7 days.

In several of his laboratory experiments, Nicholson examined the effect of delayed density dependence on blowfly population dynamics. In the first of the two experiments that we will consider here, Nicholson provided adult blowflies with unlimited food (ground liver) but restricted maggots to 50 g of food per day. Because adults had abundant food, each female was able to lay many eggs. Thus, when there were many adults, enormous numbers of eggs were produced. When those eggs hatched, however, lack of food caused most or all of the maggots to die before they reached adulthood (**Figure 11.11A**). As a result, few adults were produced, and the adult population invariably declined after reaching a peak. Eventually, the number of adults in the population reached such low levels that the few eggs they produced were able to give rise to a new generation of adults. Once this happened, the number of adults would begin to rise again, then crash, repeating the cycle just described.

Nicholson argued that delayed density dependence caused the number of adult blowflies to rise and fall repeatedly in this experiment. His reasoning was that because adults had unlimited food, the negative effects of high adult densities were not felt until a later time—that is, when the maggots hatched and began to feed. To test this idea, Nicholson performed a second experiment in which he removed some of the effects of delayed density dependence by providing both adults and maggots with a limited amount of food. When he did this, the adult population size no longer repeatedly rose and crashed. Instead, the number of adults increased and then fluctuated around an average of about 4,000 flies (**Figure 11.11B**). Taken together, the results shown in Figure 11.11 suggest that delayed density dependence can play a role in causing the pronounced fluctuations seen in some populations.

Delayed density dependence and other factors can cause a population to fluctuate in size because they can cause the growth, survival, or reproduction of individuals to vary over time, and that, in turn, can cause the population growth rate (λ) to vary significantly from one time period to the next. Next, we'll explore how such fluctuations in λ affect the risk that a population will become extinct.

CONCEPT 11.3

The risk of extinction increases greatly in small populations.

Population Extinction

Populations can be driven to extinction by many different factors, including predictable, or deterministic, changes in the environment. Consider a fish population that colonizes a temporary pond (one that forms during the rainy season but then dries out completely at other times of the year). The fish may thrive for a while, but as the water level drops, they are doomed. While such deterministic extinctions are both common and important, they are not our focus here. In this section, we'll look at how fluctuations in population growth rate, population size, and chance events in the environment affect a population's risk of extinction.

To set the stage for this discussion, let's consider a version of the geometric growth equation (Equation 10.1: $N_{t+1} = \lambda N_t$) that includes random variation in the finite rate of increase, λ. From year to year, random changes in features of the environment (e.g., weather) may cause λ to fluctuate. There will be good years, in which λ is above its average value, and bad years, in which λ is below its average value.

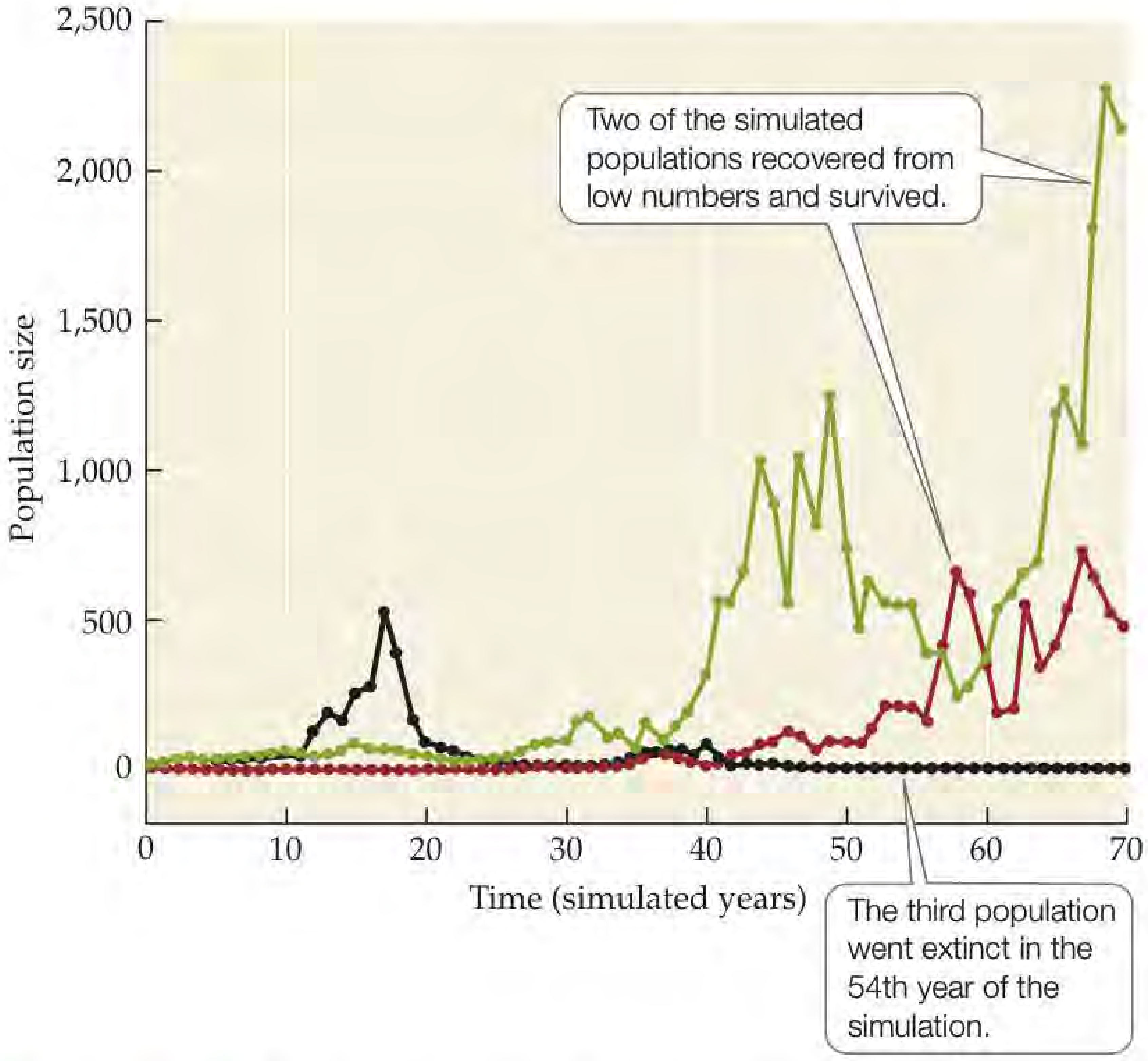


Figure 11.12 Fluctuations Can Drive Small Populations Extinct Simulated growth of three populations whose abundances changed according to the geometric growth equation ($N_{t+1} = \lambda N_t$) but in which the values of λ varied at random from year to year. This variation in λ over time was intended to simulate random variation in environmental conditions. Each simulated population began with ten individuals. For each of the three simulated populations shown here, the median value of λ was 1.05 and the standard deviation of λ was 0.4. Over time, roughly 70% of the simulated values of λ were between λ = 0.70 and λ = 1.57.

Imagine a population for which the average value of λ is greater than 1. If the value of λ fluctuates very little over time, then in most years λ will be greater than 1, and hence the population will usually increase in size. Under these circumstances, the population will deviate only slightly from a geometric growth pattern, and it will face little or no risk of extinction. However, if random variation in environmental conditions causes λ to change considerably from year to year, the population will fluctuate in size. What are the implications of such fluctuations?

Fluctuation in the population growth rate can increase the risk of extinction

To show what happens when λ fluctuates, computer simulations of geometric growth were performed for three populations in which λ was allowed to fluctuate at random. If we examine the results in **Figure 11.12**, we see that two of the populations recovered from low numbers,

ANALYZING DATA 11.1 How Does Variation in λ Affect Population Growth?

In natural populations, year-to-year estimates of the growth rate, λ, are never constant—they vary at least slightly from one year to the next. How does variation in λ affect population growth? To find out, let's compare the growth of a population in which λ has a constant value of 1.02 with the growth of a population in which λ varies over time yet has the same (average) value of λ = 1.02.

As a first step, fill in the five missing values of λ in the table, using the equation

$$\lambda = \frac{N_{t+1}}{N_t}$$

where N_t is the population size at time t (see Concept 10.3). For example, in year 0, the population size (N_0) equals 1,000; one year later, $N_1 = 820$. Thus, the first estimate of λ (indicating the change in population size from time 0 to time 1) equals $N_1/N_0 = 820/1{,}000 = 0.82$. Compute the missing values of λ, rounding each estimate to two decimal places. Check that the average (the *arithmetic mean*, defined below) of the seven values of λ equals 1.02. If it does not, redo your calculations.

YEAR (t)	POPULATION SIZE (N_t)	YEARLY GROWTH RATE (λ)
0	1,000	0.82
1	820	0.91
2	746	?
3	910	?
4	792	?
5	927	?
6	946	?
7	1,069	N/A

1. Use Equation 10.2 to calculate how large a population with a fixed growth rate of λ = 1.02 and an initial size of 1,000 ($N_0 = 1{,}000$) will be after $t = 7$ years. Compare your answer with the value shown in the table for year 7. How has year-to-year variation in λ affected the growth of the population?
2. For multiplicative processes such as population growth, an alternative is to use the *geometric mean* (defined below and described more fully in **Web Extension 11.1**) instead of the arithmetic mean. Calculate the geometric mean of the 7 year-to-year values of λ in the table.
3. Use the geometric mean that you determined in Question 2 to calculate how large a population with an initial size of 1,000 will be after 7 years. Compare your answer with the data in the table and with your result in Question 1 (which was based on the arithmetic mean).
4. Explain why you agree or disagree with this statement: "It is wrong to use the arithmetic mean of year-to-year values of λ to describe the growth of a population in a variable environment; instead, use the geometric mean."

Definitions:

Arithmetic mean: For n data points $x_1, x_2, x_3, \ldots, x_n$, the arithmetic mean equals

$$\frac{(x_1 + x_2 + x_3 + \ldots + x_n)}{n} = \frac{1}{n}\sum_{i=1}^{n} x_i$$

Geometric mean: For n data points $x_1, x_2, x_3, \ldots, x_n$, the geometric mean equals the nth root of the multiplicative product of these data points, or

$$\sqrt[n]{(x_1 \times x_2 \times x_3 \times \ldots \times x_n)}$$

See the companion website for a similar ANALYZING DATA exercise.

but one went extinct. These results support what common sense tells us: fluctuations increase the risk of extinction. In part, this occurs because a population in which λ changes over time grows more slowly than we would predict from the arithmetic mean of its year-to-year values of λ. We'll examine how adding variation to λ slows population growth in **Analyzing Data 11.1**. Such a slowdown reduces the size of the population, perhaps thereby increasing its risk of extinction.

A second (and related) factor is the extent to which the population growth rate fluctuates over time. The extent of variation in λ in the simulations was determined by a variable controlled in those simulations, the standard deviation (σ) of the growth rate. In each of the three simulated populations shown in Figure 11.12, σ was set to 0.4. (See **Web Stats Review 1.2.2** for more information about the standard deviation.)

To examine the effect of variation in λ more fully, we used the approach illustrated by Figure 11.12 to simulate 10,000 populations whose growth rates (λ) varied from year to year. Each of these 10,000 populations began with ten individuals, and in each population, λ had a median value of 1.05 and a standard deviation of σ = 0.2. With this amount of variation in λ, only 0.3% of the populations went extinct in 70 years. When σ was increased to 0.4, however, 17% of the 10,000 populations went extinct in 70 years, and when it was increased still further to σ = 0.8, 53% of the populations went extinct.

The take-home message provided by these simulations is that when variable environmental conditions increase the extent to which a population's growth rate fluctuates over time, the risk of extinction also increases. This effect, however, is dependent on the size of the population: small populations are at particular risk.

Small populations are at much greater risk of extinction than large populations

The size of a population has a strong effect on its risk of extinction. As we saw in the previous section, when we simulated the fates of 10,000 populations in which the standard deviation of λ was 0.8, 53% of those populations, each of which began with 10 individuals, became extinct in 70 years. However, when we increased the initial population size to 100 and performed the simulation again, the chance of extinction dropped from 53% to 29%. For initial population sizes of 1,000 or 10,000 individuals, the chance of extinction continued to fall (to 14% and 6%, respectively).

The simulation results we have just described suggest that small populations are much more prone to extinction than large populations. To see why, imagine that poor weather causes the growth rate (λ) of a population to be between 0.2 and 0.5 for 3 years in a row, thus causing the population to shrink considerably in size in each of those 3 years. In such a situation, a population with 10 individuals could easily be driven to extinction, whereas a population with 10,000 individuals would have survivors when conditions improved.

Similar patterns have been observed in real populations. For example, Jones and Diamond (1976) studied extinction in bird populations on the Channel Islands, located off the coast of California. By combining data from published articles (from 1868 on), museum records, unpublished field observations, and their own fieldwork, they showed that population size had a strong effect on the chance of extinction (**Figure 11.13**). They found that 39% of populations with fewer than 10 breeding pairs went extinct, whereas they observed no extinctions in populations with over 1,000 breeding pairs. Similar work by Pimm et al. (1988) showed that small populations can go extinct very rapidly: on islands off the coast of Britain, bird populations with 2 or fewer nesting pairs had a mean time to extinction of 1.6 years, while populations with 5–12 nesting pairs had a mean time to extinction of 7.5 years.

These findings for birds have been confirmed in other groups of organisms, including mammals, lizards, and insects. Overall, field data indicate that the risk of extinction increases greatly when population size is small. But what are the factors that place small populations at risk?

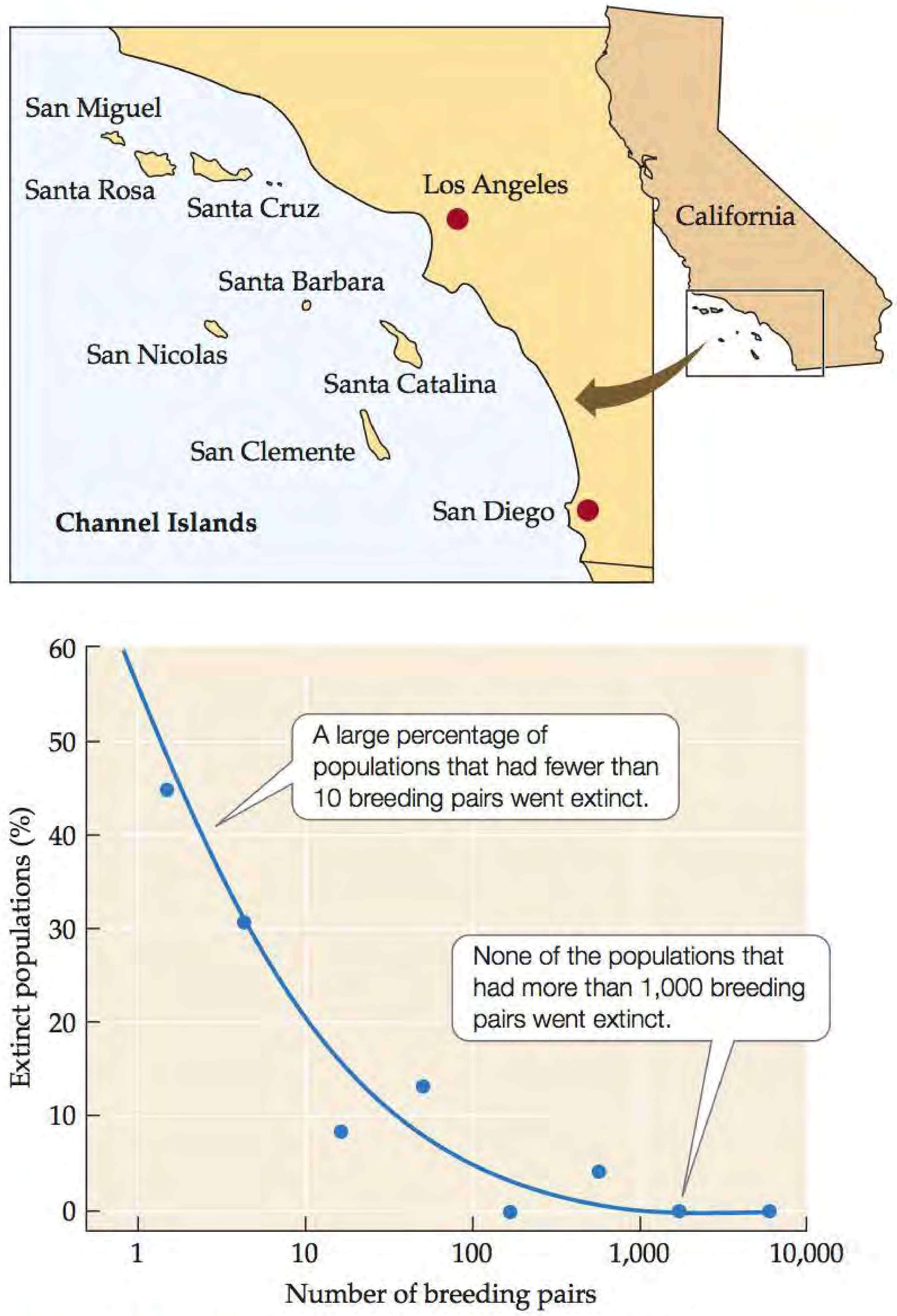


Figure 11.13 Extinction in Small Populations Among bird populations on the Channel Islands, the percentage of populations that went extinct declined rapidly as the number of breeding pairs in the population increased. (After Jones and Diamond 1976.)

? Assume that a population is at high risk (>30%) of extinction. Use the graph to estimate the total number of breeding pairs the population should have to reduce its risk of extinction to 5%.

Chance events can drive small populations to extinction

If we could predict in advance how factors that influence the survival and reproduction of individuals would vary from one year to the next, we could also predict how population growth rates would change over time. But we cannot do this in real populations. There are too many factors that we cannot predict accurately, including variation in environmental conditions (e.g., temperature and rainfall) and variation in the fates of individuals (e.g., a pollinator such as a bee might land on plant A or plant B, thereby giving one individual, but not the other, the chance to reproduce). For simplicity, in the discussion that follows, we'll refer to such unpredictable events as "chance events," even though they may ultimately have a deterministic cause. In particular, we'll consider the roles of chance genetic, demographic, and environmental events in making small populations vulnerable to extinction.

THREATS FROM GENETIC FACTORS Small populations can encounter problems associated with genetic drift and inbreeding. Recall from Concept 6.2 that *genetic drift* is the process by which chance events influence which alleles are passed on to the next generation. Genetic drift can occur in many ways, including chance events that

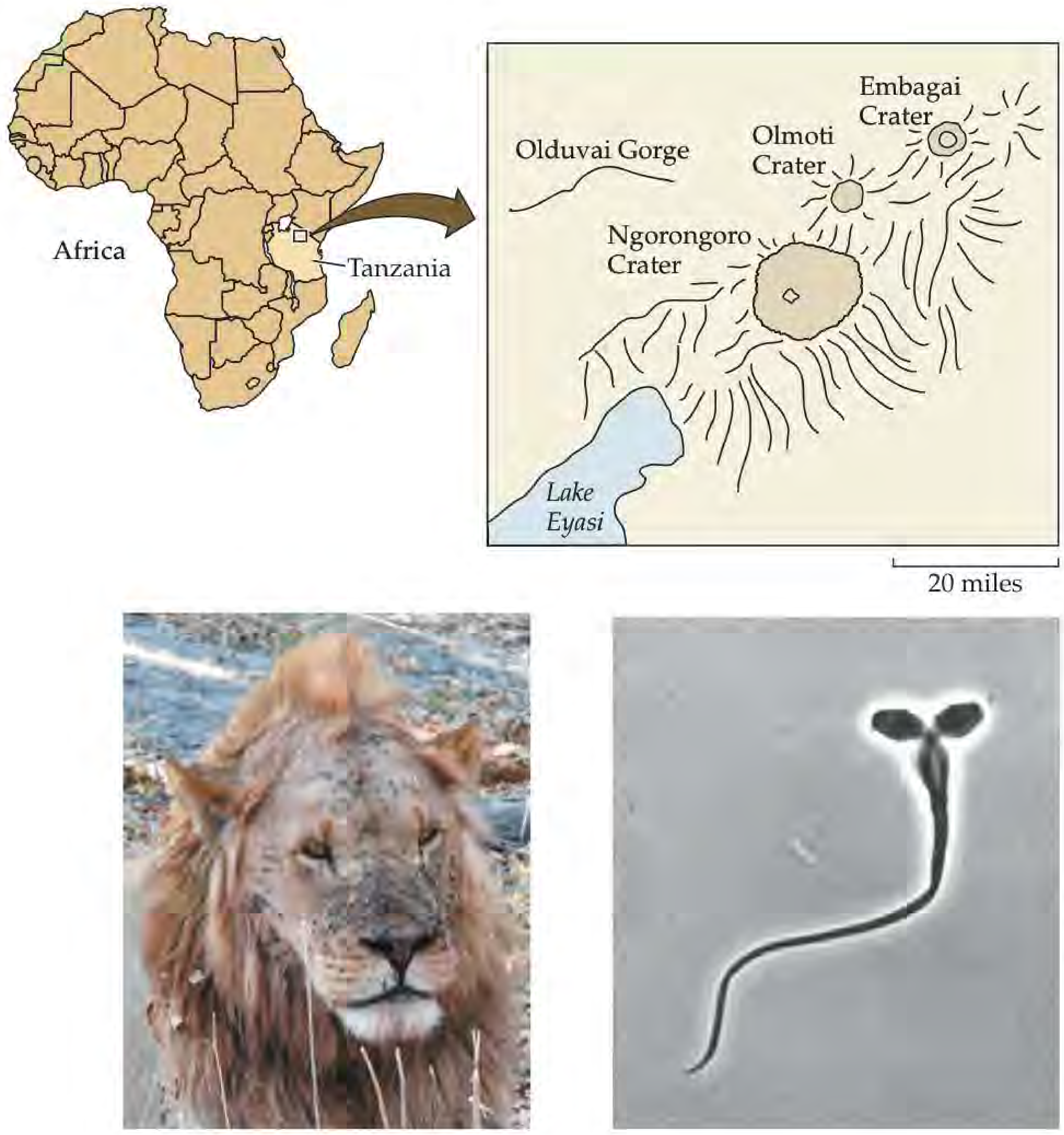


Figure 11.14 A Plague of Flies In 1962, the population of lions in the 260 km^2 (100-square-mile) Ngorongoro Crater of Tanzania was nearly driven to extinction by a catastrophic outbreak of biting flies similar to those on the face of this male. Lions became covered with infected sores and eventually could not hunt, resulting in many deaths. In the population that descended from the few survivors, genetic drift and inbreeding have led to frequent sperm abnormalities, such as this "two-headed" sperm.

determine whether individuals reproduce or die. Imagine, for example, that an elephant walks through a population of ten small plants, 50% of which have white flowers (genotype *aa*) and 50% of which have red flowers (*AA*). If the elephant happens to crush more red-flowered than white-flowered plants, then by chance alone, there will be more copies of the *a* allele than of the *A* allele in the next generation. This scenario is just one of many possible examples of how genetic drift can cause allele frequencies to change at random from one generation to the next.

Genetic drift has little effect on large populations, but in small populations it can cause losses of genetic variation over time. For example, if genetic drift causes the frequency of two alleles (e.g., *A* and *a*) to change at random in each generation, one allele may eventually increase to a frequency of 100% (reach *fixation*), while the other is lost (see Figure 6.7). Drift can reduce the genetic variation of small populations rapidly: for example, after ten generations, roughly 40% of the original genetic variation is lost in a population of ten individuals, while 95% is lost in a population of two individuals.

Small populations are vulnerable to extinction caused by genetic factors for three reasons. First, when genetic drift leads to a loss of genetic variation, the ability of a population to respond (via natural selection) to future environmental change is limited. Second, genetic drift can cause harmful alleles to occur at high frequencies, often causing individuals to suffer poor reproductive success (as in the case of the greater prairie chicken described in Figure 6.8). Third, small populations show a high frequency of **inbreeding** (mating between related individuals). Inbreeding is common in small populations because after several generations at a small population size, most of the individuals in the population will be closely related to one another (to see why, answer Review Question 3). Inbreeding tends to increase the frequency of homozygotes, including those that have two copies of a harmful allele. Thus, like genetic drift, inbreeding can lead to reduced reproductive success, causing birth rates, and hence population growth rates, to drop.

The combined negative effects of genetic drift and inbreeding appear to have reduced the fertility of male lions that live on the floor of the Ngorongoro Crater, Tanzania (**Figure 11.14**). From 1957 to 1961, there were 60–75 lions living in the crater, but in 1962 an extraordinary outbreak of biting flies caused all but 9 females and 1 male to die. Seven males immigrated into the crater in 1964–1965, but no further immigration has occurred since that time. The population has increased in size since the 1962 crash. From 1975 to 1990, for example, the population fluctuated between 75 and 125 individuals. However, genetic analyses indicated that all these individuals were descendants of just 15 lions (Packer et al. 1991). In a population of 15 individuals, genetic drift and inbreeding have powerful effects. Those effects appear to be the reason why the crater population has less genetic variation and more frequent sperm abnormalities than the large population of lions found nearby on the Serengeti Plain. In such a situation, all is not necessarily lost: in some cases, populations in decline because of drift and inbreeding have been "rescued" by introducing a small number of individuals from other, more genetically diverse populations (see Figures 6.8 and 23.16).

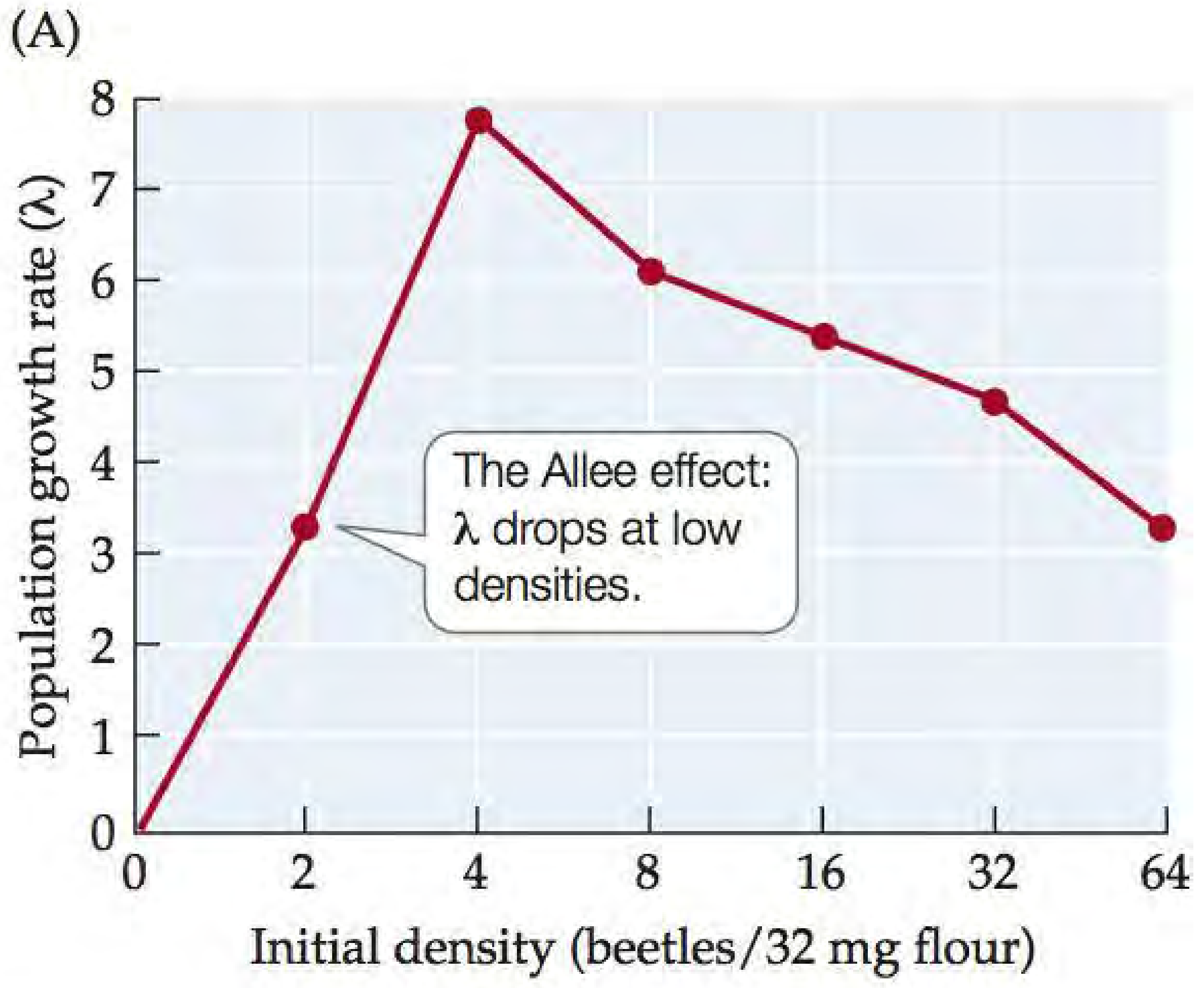
THREATS FROM DEMOGRAPHIC FACTORS For an individual, survival and reproduction are all-or-nothing events:

an individual either survives or it does not, and it either reproduces or it does not. At the population level, we can transform such all-or-nothing events into a probability that survival or reproduction will occur. For example, if 70 out of 100 individuals in a population survive from one year to the next, then (on average) each individual in the population has a 70% chance of survival.

In a small population, however, chance events related to the survival and reproduction of individuals (**demographic stochasticity**) can result in outcomes that differ from what such averages would lead us to expect. Consider a population of ten individuals for which previous data indicate that, on average, each individual has a 70% probability of surviving from one year to the next. However, many chance events—such as whether an individual is struck by a falling tree—can cause the percentage of individuals that actually do survive to be higher or lower than 70%. For example, if six of the ten individuals experienced (the ultimate) "bad luck" and died in chance mishaps, the observed survival rate (40%) would be much lower than the expected 70%. By affecting the survival and reproduction of individuals in this way, demographic stochasticity can cause the size of a small population to fluctuate over time. In one year the population may grow, while the next it may decrease in size, perhaps so drastically that extinction results.

In contrast, when the population size is large, there is little risk of extinction from demographic stochasticity. The fundamental reason for this has to do with laws of probability. You are, for example, much more likely to receive zero heads if you toss a fair coin 3 times than if you toss the same coin 300 times. Similarly, when we consider the demographic fates of individuals, we can see that chance events are much more likely to cause reproductive failure or poor survival in small populations than in large populations. If each individual in a population has a $1/3$ chance of producing zero offspring, then if there are 2 individuals in the population, there is an 11% chance ($0.33 \times 0.33 = 0.33^2 = 0.11$) that no offspring will be produced—driving the population to extinction in one generation. Although demographic stochasticity could cause a population of 30 individuals to fluctuate in size (perhaps leading to eventual extinction), there is essentially no chance (0.33^{30}) that it could cause the population to go extinct in a single generation.

Demographic stochasticity is also one of several factors that can cause small populations to experience Allee effects. **Allee effects** occur when the population growth rate (r or λ) *decreases* as the population density decreases, perhaps because individuals have difficulty finding mates at low population densities (**Figure 11.15**). This phenomenon reverses the usual assumption that r and λ tend to



Thunnus thynnus

Strigops habroptilus

Aconitum napellus

Figure 11.15 Allee Effects Can Threaten Small Populations Allee effects occur when the growth rate of a population decreases as population density decreases. (A) In laboratory experiments with the flour beetle *Tribolium*, population growth rates reached their lowest point at the lowest initial density. Allee effects can be important in animals such as (B) bluefin tuna (*Thunnus thynnus*), which form schools or herds whose protective or early warning systems function poorly at small population sizes. Allee effects are also important in species in which individuals have difficulty finding mates at low population densities; there are many such species, including (C) kakapos (*Strigops habroptilus*) and (D) monkshood (*Aconitum napellus*). (A after Courchamp et al. 1999.)

increase as population density decreases (see Figure 10.17). Allee effects can be disastrous for small populations. If demographic stochasticity or any other factor decreases the population size, Allee effects can cause the population growth rate to drop, which causes the population size to decrease even further in a downward spiral toward extinction.

THREATS FROM ENVIRONMENTAL VARIATION As we have stressed repeatedly, environmental conditions vary from year to year. Such variation can affect birth and death rates, leading to fluctuations in population size that can increase the risk of extinction. Our focus here will be on how two types of chance events, environmental stochasticity and natural catastrophes, can cause extinction in small populations.

Environmental stochasticity refers to erratic or unpredictable changes in the environment. In the simulations described above (see Figure 11.12), we've already seen (1) that variation in environmental conditions that causes fluctuations in population growth rates can lead to population size fluctuations and thus an increased risk of extinction, and (2) that such environmental variation is more likely to cause extinction when the population size is small. Many species face such risks from environmental stochasticity. For example, census data on female grizzly bears (*Ursus arctos horribilis*) in Yellowstone National Park showed that the average population growth rate (r) was approximately 0.02 but that it varied from year to year. Despite the fact that the population tends to grow in size (because $r > 0$), researchers using a mathematical model found that random variation in environmental conditions could place the Yellowstone grizzly population at high risk of extinction, especially if the population size were to drop to 30 or 40 females from its 1997 level of 99 females (**Figure 11.16**).

Environmental stochasticity differs from demographic stochasticity in a fundamental way. Environmental stochasticity refers to changes in the average birth or death rate of a population that occur from one year to the next. These year-to-year changes reflect the fact that environmental conditions vary over time, affecting all the individuals in a population: sometimes there are good years and sometimes there are bad years. In demographic stochasticity, the average (population-level) birth and death rates may be constant across years, but the actual fates of individuals differ because of the random nature of whether each individual reproduces or not, and survives or not.

Populations also face risks from extreme environmental events such as floods, fires, severe windstorms, or outbreaks of disease or natural enemies. Even though they occur rarely, such **natural catastrophes** can eliminate or drastically reduce the size of populations that otherwise would seem large enough to be at little risk of extinction.

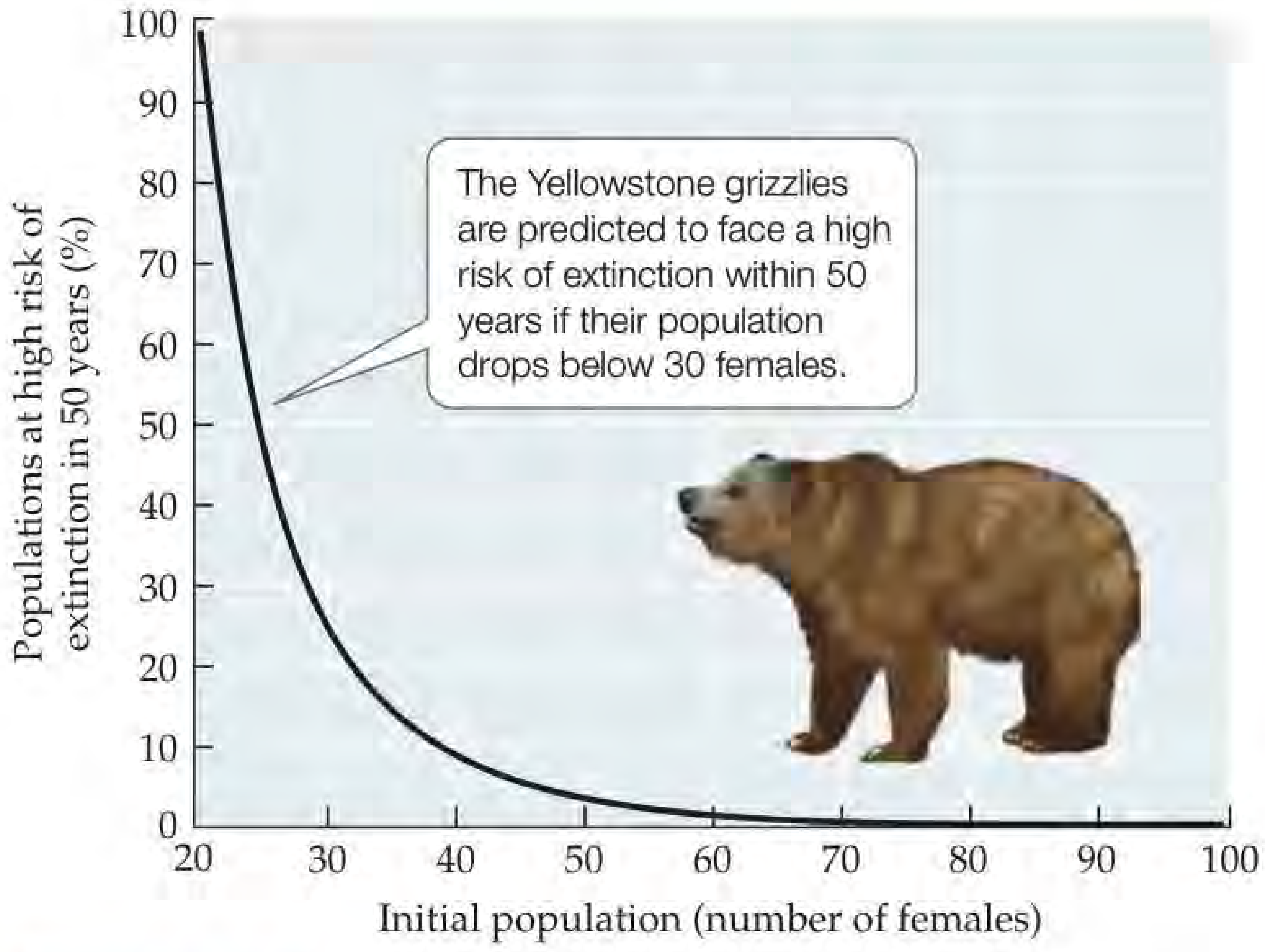


Figure 11.16 Environmental Stochasticity and Population Size This graph plots the risk that the Yellowstone grizzly bear population will be close to extinction in 50 years against the population size (number of females). By studying 39 consecutive years of census data, researchers found that the average population growth rate of Yellowstone grizzlies was $r = 0.02$—a rate that would lead to explosive growth if it remained constant from year to year. The risk of extinction was calculated from a mathematical model that examined the effect of environmental stochasticity by incorporating the variation in r observed over the 39 years of data. (After Morris and Doak 2002.)

For example, disease outbreaks have resulted in mass mortality in populations of sea urchins (up to 98% of the individuals in some populations) and Baikal seals (killing about 2,500 of a population of 3,000 seals).

Natural catastrophes also played a key role in the extinction of the heath hen (*Tympanuchus cupido cupido*). This bird was once abundant from Virginia to New England. By 1908, hunting and habitat destruction had reduced its population to 50 birds, all on the island of Martha's Vineyard, where a 1,600-acre reserve was established for its protection. Initially, the population thrived, increasing in size to 2,000 birds by 1915. A population of 2,000 may seem large enough to be nearly "bulletproof" against the problems that threaten small populations, including genetic drift and inbreeding, demographic stochasticity, and environmental stochasticity. However, a series of disasters struck between 1916 and 1920, including a fire that destroyed many nests, unusually cold weather, a disease outbreak, and a boom in the number of goshawks (a predator of heath hens). Because of the combined effects of these events, the heath hen population dropped to 50 birds by 1920 and never recovered. The last heath hen died in 1932.

With the benefit of hindsight, we can see that heath hens were vulnerable in 1915 because they all lived in a single population. More typically, members of a species are found in multiple populations, which are often isolated from one another by regions of unsuitable habitat.

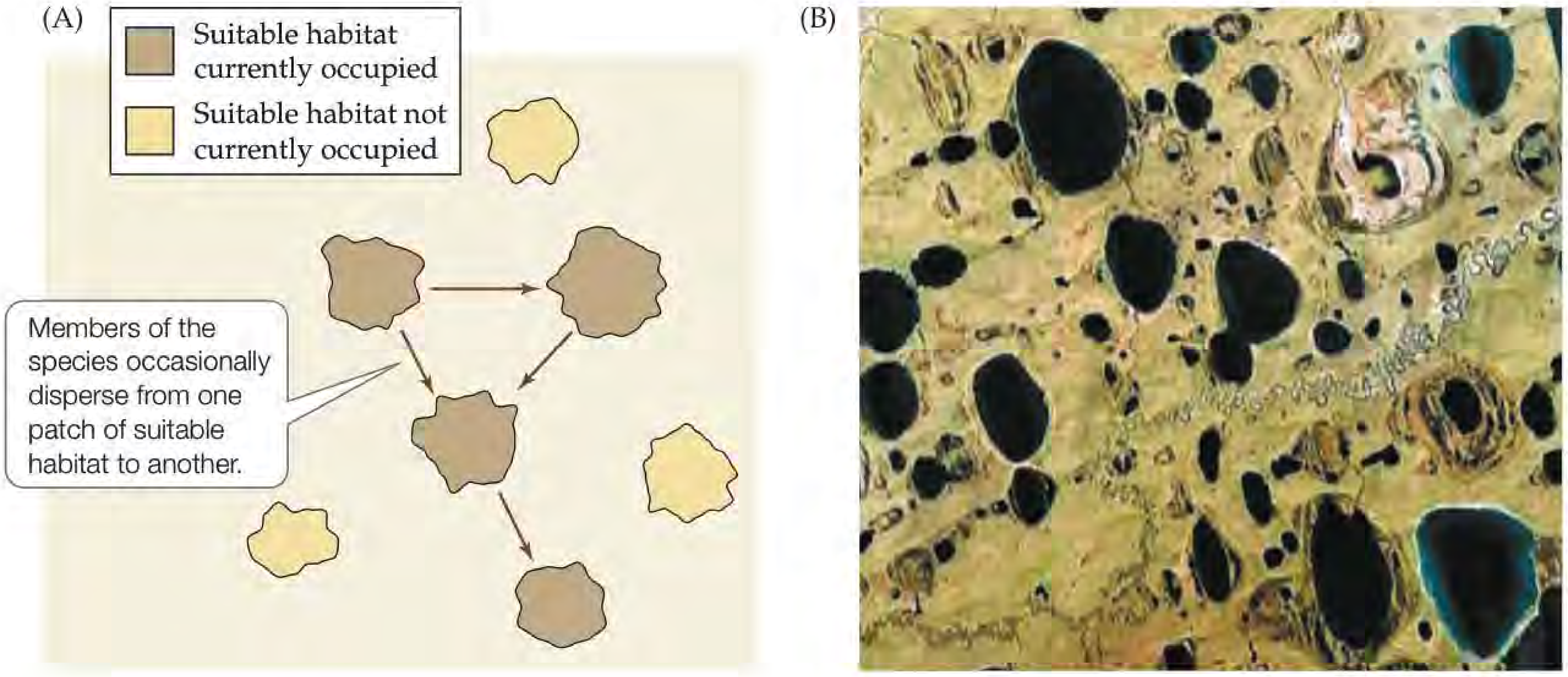


Figure 11.17 The Metapopulation Concept A metapopulation is a set of spatially isolated populations linked by dispersal. (A) Seven patches of suitable habitat for a species are diagrammed, four of which are currently occupied and three of which are not. The area outside of these seven patches represents unsuitable habitat. (B) Satellite image of a group of lakes in northern Alaska that are sometimes connected to one another by temporary streams that form after the snow melts or after periods of heavy rainfall.

CONCEPT 11.4

In metapopulations, sets of spatially isolated populations are linked by dispersal.

Metapopulations

The checkered landscapes visible in satellite photos demonstrate that the world is a patchy place (see Figure 10.1). The patchy nature of the landscape ensures that for many species, areas of suitable habitat do not cover large, continuous regions, but rather exist as a series of favorable sites that are spatially isolated from one another. As a result, the populations of a species are often scattered across the landscape, each in an area of favorable habitat but separated from one another by hundreds of meters or more.

Sometimes these spatially isolated populations are not linked by dispersal and hence do not affect one another's population dynamics. In many cases, however, seemingly isolated populations do affect one another's dynamics because individuals (or gametes) occasionally disperse from one population to another. Such a group of interacting populations is called a **metapopulation**. Literally, the term "metapopulation" refers to a population of populations, but it is usually defined in a more particular sense as a set of spatially isolated populations linked to one another by dispersal (**Figure 11.17**). In some metapopulations, certain populations are *sources* (from which the number of individuals that disperse to other populations is greater than the number of migrants they receive) while other populations are *sinks* (which receive more immigrants than the number of emigrants they produce).

Metapopulations are characterized by repeated extinctions and colonizations

As ecologists have long recognized, populations of some species are prone to extinction for two reasons: (1) the patchiness of their habitat makes dispersal between populations difficult, and (2) environmental conditions can change in a rapid and unpredictable manner. Metaphorically, we can think of such populations as a set of "blinking lights" that wink on and off, seemingly at random, as patches of suitable habitat are colonized and the populations in those patches then go extinct. Although the individual populations may be prone to extinction, the collection of populations—the metapopulation—persists because it includes populations that are going extinct and new populations established by colonization.

Building on this idea of random extinctions and colonizations, Richard Levins (1969, 1970) represented metapopulation dynamics in terms of the extinction and colonization of habitat patches:

$$\frac{dp}{dt} = cp(1-p) - ep \qquad \textbf{(11.2)}$$

where p represents the proportion of habitat patches that are occupied at time t, while c and e are the patch colonization and patch extinction rates, respectively.

In deriving Equation 11.2, Levins made a number of assumptions: (1) that there is a very large (infinite) number of identical habitat patches, (2) that all patches have an equal chance of receiving colonists (hence the spatial arrangement of the patches does not matter), (3) that all patches have an equal chance of extinction, and (4) that once a patch is colonized, its population increases to its carrying capacity much more rapidly than the rates at which extinction and colonization occur (this assumption allows population dynamics within patches to be ignored).

As we'll discuss below, some of the assumptions of Levins's model are not realistic. Still, Equation 11.2 leads to a simple but fundamental insight: for a metapopulation to persist for a long time, the ratio e/c must be less than 1 (see **Web Extension 11.2** for a description of how this result was obtained). In words, this means that some patches will be occupied if the colonization rate is greater than the extinction rate. On the other hand, if the extinction rate is greater than the colonization rate (and hence, $e/c > 1$), the metapopulation will collapse and all populations in it will become extinct. Levins's groundbreaking approach focused attention on a number of key issues, such as how to estimate factors that influence patch colonization and extinction, the importance of the spatial arrangement of suitable patches, the extent to which the landscape between habitat patches affects dispersal, and the vexing problem of how to determine whether empty patches are suitable habitat or not. Levins's rule for persistence also has applied importance, as we will see shortly.

A metapopulation can go extinct even when suitable habitat remains

Human actions (such as land development) often convert large tracts of habitat into sets of spatially isolated habitat fragments (see Figure 9.4). Such **habitat fragmentation** can cause a species to have a metapopulation structure where it did not have one before. If land development continues and the habitat becomes still more fragmented, the metapopulation's colonization rate (c) may decrease because patches become more isolated and hence harder to reach by dispersal. Further habitat fragmentation also causes the patches that remain to become smaller; as a result, the extinction rate (e) may increase because smaller patches have smaller populations, which, as we have just seen, have a higher risk of extinction. Both of these trends (an increase in e and a decrease in c) cause the ratio e/c to increase. Thus, if too much habitat is removed, the ratio e/c may shift suddenly from less than 1 to greater than 1, thereby dooming all populations—and the metapopulation—to eventual extinction, even though some habitat remains.

The idea that all populations in a metapopulation might go extinct while suitable habitat remains was developed further in studies on the northern spotted owl (**Figure 11.18**). The northern spotted owl (*Strix occidentalis caurina*) is found in the Pacific Northwest region of North America. It lives in old-growth forest, where nesting pairs establish large territories that range in size from 12 to 30 km^2 (territories are larger in poor-quality habitat). Lande (1988) modified Levins's model to include a description of how owls might search for vacant "patches," which were interpreted as sites suitable for individual territories. Lande estimated that the entire metapopulation would collapse if the area covered by old-growth forest were reduced by logging to less than 20% of the total area of a large region. This result had a powerful impact: it illustrated how a species might go extinct if its habitat dropped below a critical threshold (in this case, 20% suitable habitat), and it contributed to the 1990 listing of the northern spotted owl as a threatened species in the United States. The importance of conserving old-growth forest has been highlighted by the effects of a recent invader, the barred owl (*Strix varia*): the arrival of this species can cause spotted owl populations to become extinct, but such extinctions are less likely in old-growth forests that cover a large area (Dugger et al. 2011).

Figure 11.18 The Northern Spotted Owl The northern spotted owl (*Strix occidentalis caurina*) thrives in old-growth forests of the Pacific Northwest; such forests include those that have never been cut, or have not been cut for 200 years or more.

Extinction and colonization rates often vary among patches

As the impact of Lande's work on the northern spotted owl suggests, the metapopulation approach has become increasingly important in applied ecology. But metapopulations in the field often violate the assumptions of Levins's model. For example, patches often differ considerably in population size and in the ease with which they can be reached by dispersal. As a result, extinction and colonization rates may vary greatly among patches. Therefore, most ecologists use more complex models (see Hanski 1999) when addressing practical questions in the field.

Consider the skipper butterfly *Hesperia comma*. In the early 1900s, this butterfly was found on grazed calcareous grasslands (i.e., grasslands growing in alkaline soils found on limestone or chalk outcrops) throughout a broad range of the United Kingdom. Starting in the 1950s, however, calcareous grasslands became overgrown because the numbers of cattle and other important grazers were reduced. As a result, *H. comma* populations began to decline. By the mid-1970s, the butterfly was found in only ten restricted regions, a very small fraction of its original range.

Things began to pick up for the butterfly in the early 1980s. By this time, habitat conditions had improved because livestock had been reintroduced. Surveying these grasslands in 1982, Chris Thomas and Terésa Jones documented the locations of all patches containing *H. comma* populations and of all patches that appeared suitable for, but were not occupied by, *H. comma*. To determine the fate of each occupied and unoccupied patch over time, they surveyed the patches again in 1991 and noted which ones were occupied at that time. Their results highlight two important features of many metapopulations: isolation by distance and the effect of patch area.

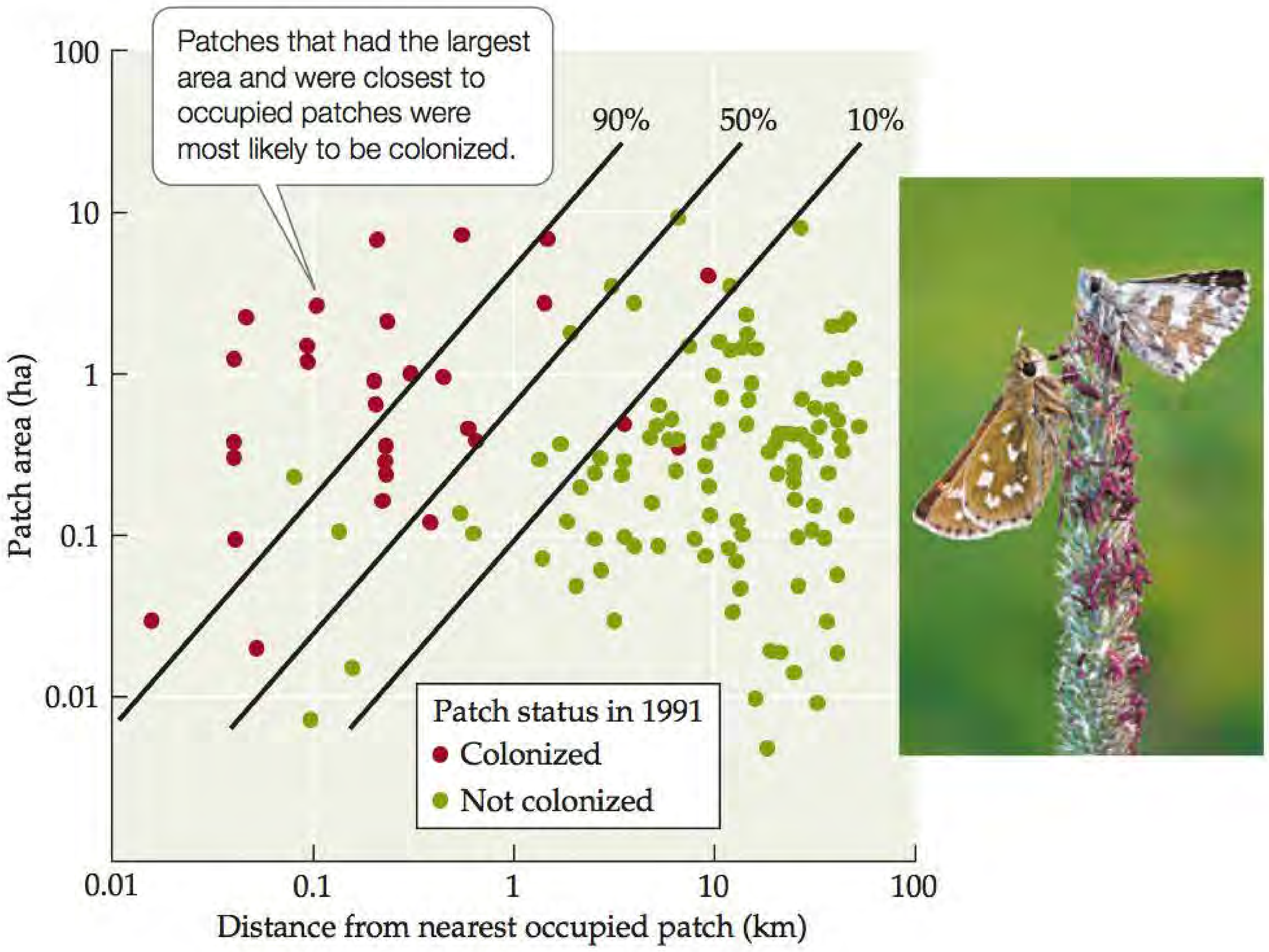


Figure 11.19 Colonization in a Butterfly Metapopulation Colonization of suitable habitat from 1982 to 1991 by the skipper butterfly *Hesperia comma* was influenced by patch area and patch isolation (distance to the nearest occupied patch). Each red or green circle represents a patch of suitable habitat that was not occupied by *H. comma* in 1982. The lines show the combinations of patch area and patch isolation for which there was a 90%, 50%, and 10% chance of colonization (as calculated from a statistical analysis of the data). (After Thomas and Jones 1993.)

? Based on these results, estimate the chance of colonization for a 1 ha patch located 1 km away from the nearest occupied patch.

Isolation by distance occurs when patches located far from occupied patches are less likely to be colonized than are nearby patches. In *H. comma*, distance from occupied patches had a strong effect on whether patches vacant in 1982 were colonized by 1991: few patches separated by more than 2 km from an occupied patch were colonized during that period (**Figure 11.19**). Patch area also affected the chance of colonization: the majority of colonized patches were at least 0.1 hectare (ha) in size. Patch area may have affected colonization rates directly because small patches may be harder for the butterflies to find than large patches. Alternatively, *H. comma* might have colonized small patches, but then suffered extinction in those patches by 1991 due to problems associated with small population size; such patches would appear never to have been colonized because the sites were not sampled between 1982 and 1991.

Among patches occupied in 1982, Thomas and Jones found that the chance of extinction was highest in small patches (most likely because small patches tend to have small population sizes) and in patches that were far from another occupied patch. Isolation by distance can affect the chance of extinction because a patch that is near an occupied patch may receive immigrants repeatedly, which may increase the patch population size and make extinction less likely. This tendency for high rates of immigration to protect a population from extinction (by reducing the problems associated with small population size) is known as the **rescue effect** (Brown and Kodric-Brown 1977).

Finally, extinction and colonization can be influenced by nonrandom components of the environment. For example, primroses (*Primula vulgaris*) colonize patches on the forest floor where windstorms or other factors have killed trees, producing openings in the tree canopy above. While patch colonization by primroses can be viewed as a random event, patch extinction is not: as the forest regrows, the canopy closes, and the primroses die from lack of sunlight (Valverde and Silvertown 1997). Colonization can also be influenced by nonrandom features of the environment. Some ponds, for example, consistently provide better habitat than others. The high quality of the habitat in such ponds enables frogs and other aquatic animals that colonize them to produce many offspring, and that in turn increases the chance that a new population will establish itself successfully.

A CASE STUDY REVISITED

A Sea in Trouble

In the late 1980s and early 1990s, the Black Sea ecosystem was under severe duress from the combined effects of eutrophication and invasion by the comb jelly *Mnemiopsis leidyi*, as described in the Case Study. Although *Mnemiopsis* numbers declined sharply in 1991, they rose steadily again from 1992 to 1995, and then remained high for several years—at about 250 g per square meter, which translates to over 115 million tons of *Mnemiopsis* throughout the Black Sea. The situation did not look promising. But by 1999, matters were different: the Black Sea was showing signs of recovery.

The events that set the stage for the recovery of the Black Sea actually began prior to the first onslaught of *Mnemiopsis*. In the mid- to late 1980s, the amounts of nutrients added to the Black Sea began to level off. From 1991 to 1997, nutrient inputs declined, probably because of hard economic times in former Soviet Union countries coupled with national and international efforts to reduce

Figure 11.20 Invader versus Invader Another invasive comb jelly species, the predator *Beroe*, brought *Mnemiopsis* under control, thus contributing to the recovery of the Black Sea ecosystem.

nutrient inputs. The reduction had rapid effects: after 1992, phosphate concentrations in the Black Sea declined, phytoplankton biomass began to fall, water clarity increased, and zooplankton abundance increased. *Mnemiopsis* still posed a threat, however, as evidenced by its high biomass and by falling anchovy catches from 1995 to 1998 (see Figure 11.2). Scientists and government officials were gearing up to combat the threat from *Mnemiopsis* when the problem was inadvertently solved by the arrival of another comb jelly, the predator *Beroe* (**Figure 11.20**).

Beroe arrived in 1997. Like *Mnemiopsis*, *Beroe* probably reached the Black Sea in the ballast water of ships from the Atlantic. *Beroe* feeds almost exclusively on *Mnemiopsis*. It is such an effective predator that within 2 years of its arrival, *Mnemiopsis* numbers plummeted (see Figure 11.2A). Following the sharp decline in *Mnemiopsis*, the Black Sea population of *Beroe* also crashed, presumably because it depended on *Mnemiopsis* for food. The fall of *Mnemiopsis* led to a rebound in zooplankton abundance (which had dropped again from 1994 to 1996) and to increases in the population sizes of several native jellyfish species. In addition, after the *Mnemiopsis* population crashed, there was an increase in the anchovy catch and in field counts of anchovy egg densities. Overall, the decline of *Mnemiopsis* helped to improve the condition of the Black Sea ecosystem, including the fisheries on which people depend for food and income.

CONNECTIONS IN NATURE
From Bottom to Top, and Back Again

The decrease in nutrient inputs by human activities and the control of *Mnemiopsis* by *Beroe* had rapid beneficial effects on the entire Black Sea ecosystem. The speed and magnitude of the ecosystem's recovery provide a source of hope, suggesting that it may be possible to solve large problems in other aquatic communities. Note, however, that ecologists rarely attempt to solve such problems by deliberately introducing new predators, such as *Beroe*, because such introductions often have unanticipated negative effects.

The details of the fall and rise of the Black Sea ecosystem also illustrate two important types of causation in ecological communities: bottom-up and top-down controls. The fall of the Black Sea ecosystem began when increased nutrient inputs led to problems associated with eutrophication: increased phytoplankton abundance, increased bacterial abundance, decreased oxygen concentrations, and fish die-offs. The effect of adding nutrients to the Black Sea illustrates **bottom-up control**, which occurs when the abundance of a population is limited by nutrient supply or food availability. In this case, prior to nutrient enrichment, phytoplankton abundance—and thus the abundance of food for other organisms—was limited by the supply of nutrients.

Ecosystems are also affected by **top-down control**, which occurs when the abundance of a population is limited by predators. Recent evidence indicates that early steps in the decline of the Black Sea ecosystem were driven not only from the bottom up (by eutrophication), but also from the top down, by overfishing (Daskalov et al. 2007). Starting in the late 1950s, overfishing caused sharp drops in the abundances of predatory fishes. As predatory fish populations declined, their prey, planktivorous (plankton-eating) fishes, increased in number (**Figure 11.21A**). In turn, the increase in planktivorous fishes was associated with declining numbers of zooplankton and increasing numbers of phytoplankton (**Figure 11.21B,C**), suggesting possible top-down control. Later, the arrival of the voracious predator *Mnemiopsis* also had a top-down effect, altering many key features of the ecosystem (e.g., zooplankton abundance, phytoplankton abundance, fish abundance). Top-down control also seems to have influenced ecosystem recovery: it took another predator, *Beroe*, to rein in *Mnemiopsis*. In many cases, as in the Black Sea, bottom-up and top-down controls interact to shape how ecosystems work. We'll return to bottom-up and top-down controls in Units 5 and 6, where we consider these important topics in more detail.

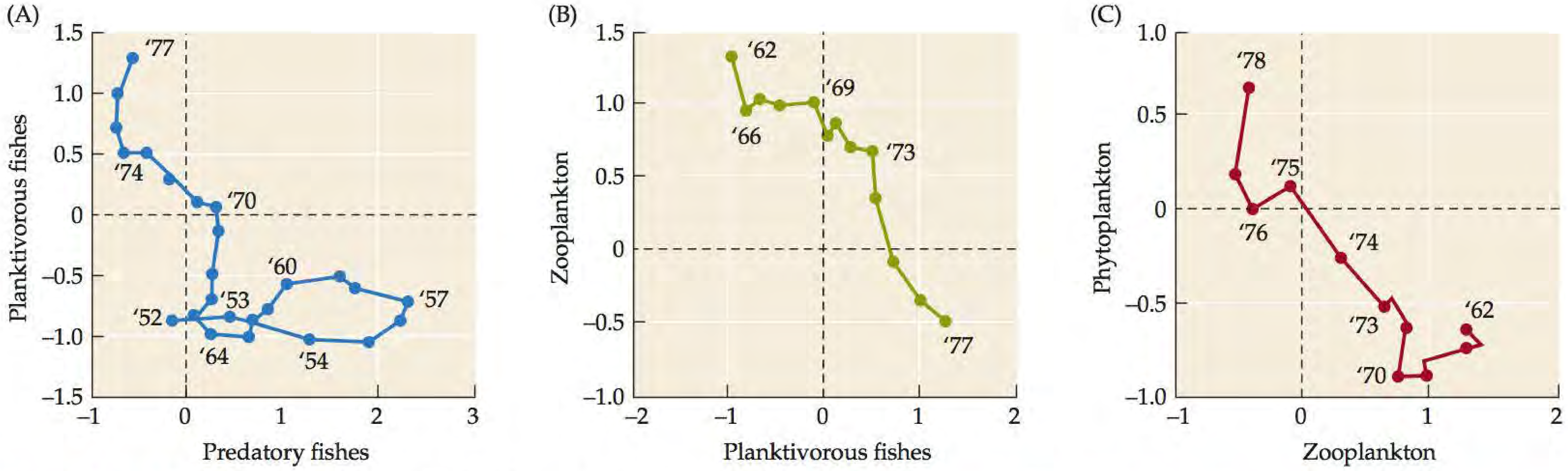


Figure 11.21 Ecosystem Changes in the Black Sea Abundance indices of (A) planktivorous and predatory fishes, (B) zooplankton and planktivorous fishes, and (C) phytoplankton and zooplankton. In each graph, the organisms whose abundance is plotted on the *y* axis are eaten by the organisms whose abundance is plotted on the *x* axis. (Planktivorous fishes eat both zooplankton and phytoplankton, but they have a greater effect on zooplankton abundance than on phytoplankton abundance.) Numbers on the plots indicate years, beginning in 1952. In the abundance indices, data are standardized to have a mean of 0 and a variance of 1 (see **Web Stats Review 1.2** to learn how and why this is done). (After Daskalov et al. 2007.)

? Referring to (A), describe predatory and planktivorous fish abundance from 1952 to 1957. Next, summarize how abundances of phytoplankton, zooplankton, planktivorous fishes, and predatory fishes changed in the 1970s. Finally, convert your summary of abundance changes in the 1970s into a chain of feeding relationships, where arrow thickness indicates the strength of each relationship (see Figure 9.21, in which similar chains are shown for Alaska). Is the chain you drew more similar to that in Alaska pre-1990 or that in Alaska in the late 1990s? Explain.

Summary

CONCEPT 11.1 Population growth patterns include exponential growth, logistic growth, fluctuations, and regular cycles.

- Most observed patterns of population growth can be grouped into four major types: exponential growth, logistic growth, fluctuations, and regular cycles. These four patterns are not mutually exclusive, and a single population can experience each of them at different times.
- The first pattern, exponential growth, can occur for a limited time when conditions are favorable.
- The second pattern, logistic growth, is found in populations that increase initially and then level off at a maximum population size, the carrying capacity.
- The third pattern, population fluctuations, is found in all populations. Some populations fluctuate greatly over time; others fluctuate relatively little.
- The fourth pattern, regular population cycles, is a special type of fluctuation in which alternating periods of high and low abundance occur after nearly constant intervals of time.

CONCEPT 11.2 Delayed density dependence can cause populations to fluctuate in size.

- There is often a time lag between a change in population density and the effect that change has on future population densities.
- A version of the logistic equation that includes a time lag suggests that delayed density dependence can produce several types of population fluctuations, including damped oscillations and stable limit cycles.
- A series of pioneering experiments by A. J. Nicholson indicated that delayed density dependence was a cause of fluctuations in laboratory blowfly populations.

CONCEPT 11.3 The risk of extinction increases greatly in small populations.

- The risk of extinction increases in populations whose growth rate (λ) varies considerably from one year to the next.
- Small populations are at much greater risk of extinction than large populations.
- Small populations can be driven to extinction by chance events associated with genetic drift and inbreeding, demographic stochasticity, environmental stochasticity, and natural catastrophes.

CONCEPT 11.4 In metapopulations, sets of spatially isolated populations are linked by dispersal.

- Metapopulations are sets of populations that are spatially isolated but linked by dispersal. They are characterized by repeated extinctions and colonizations of the isolated populations.
- A metapopulation can be doomed to extinction even when some suitable habitat remains.
- Extinction and colonization rates often vary among a metapopulation's patches.