CARL T. BERGSTROM • LEE ALAN DUGATKIN

evolution

SECOND EDITION

EVOLUTION

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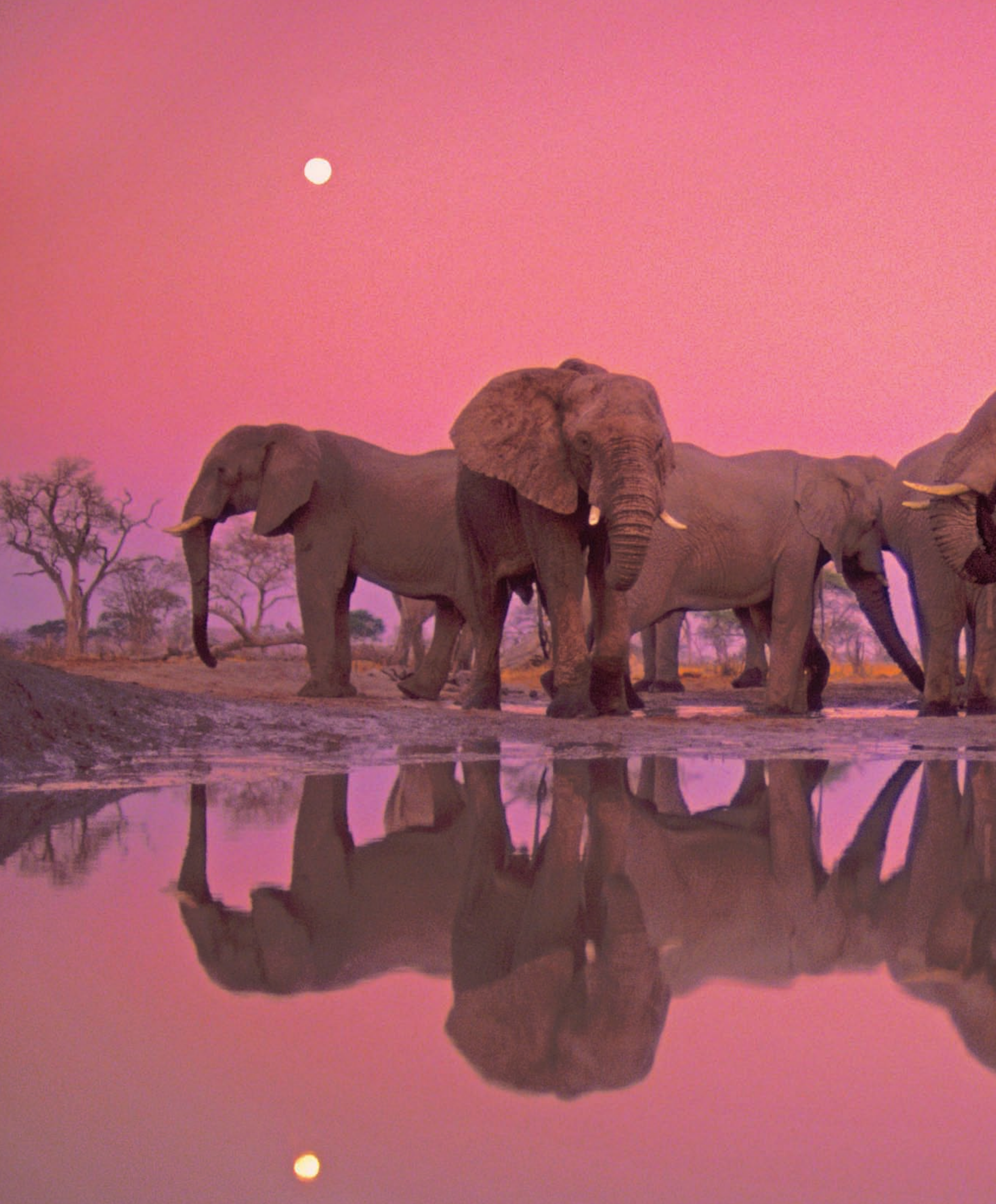

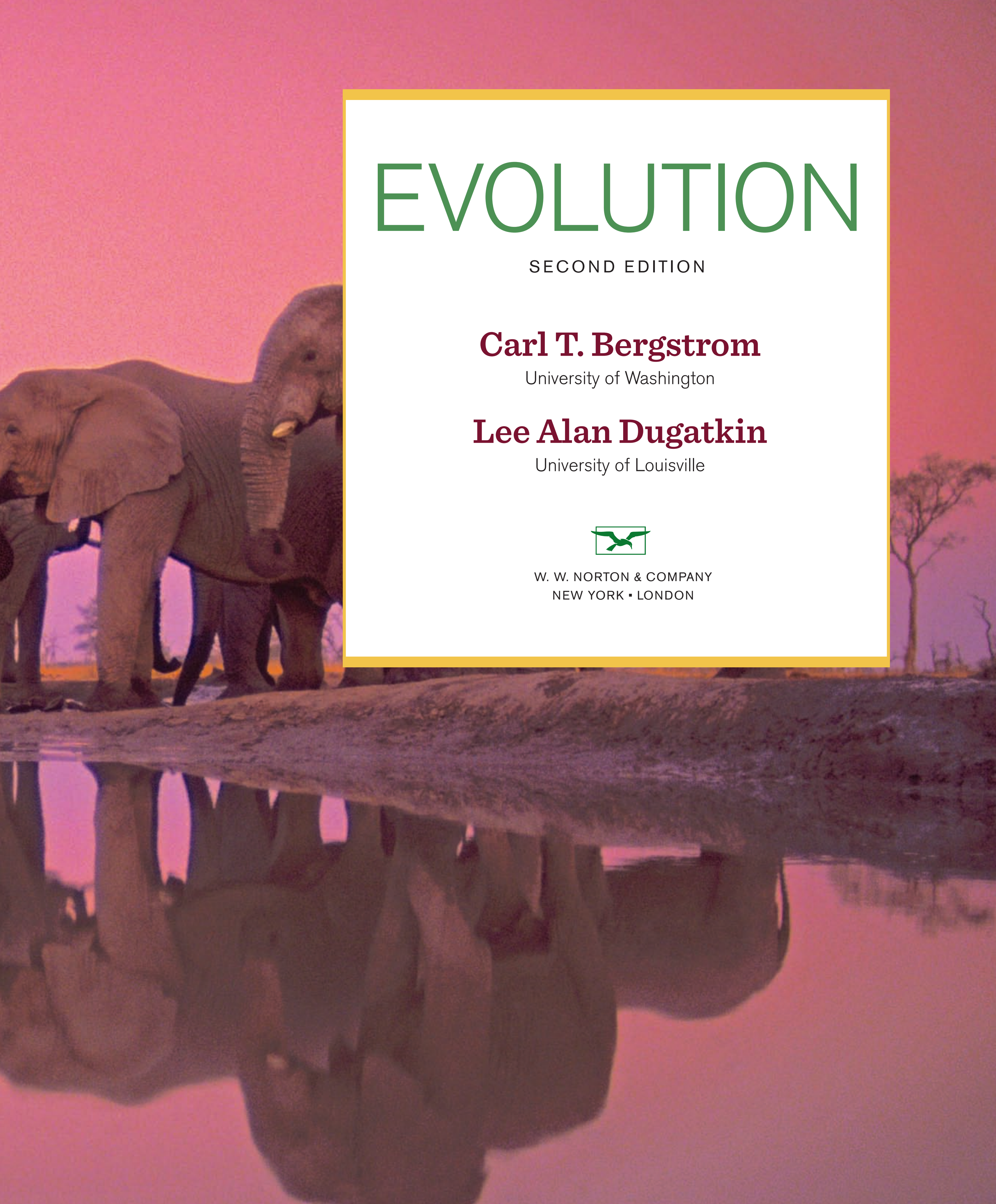

EVOLUTION

SECOND EDITION

Carl T. Bergstrom
University of Washington

Lee Alan Dugatkin
University of Louisville

W. W. NORTON & COMPANY
NEW YORK • LONDON

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PART IV
Evolutionary Interactions

ABOUT THE AUTHORS

Carl T. Bergstrom is a professor in the Department of Biology at the University of Washington in Seattle. Dr. Bergstrom's research uses mathematical, computational, and statistical models to understand how information flows through biological and social systems. His recent projects include contributions to the game theory of communication and deception, application of information theory to the study of evolution by natural selection, and development of mathematical techniques for mapping and comprehending large network data sets. In the applied domain, Dr. Bergstrom's work illustrates the value of evolutionary biology for solving practical problems in medicine and beyond. These problems include dealing with drug resistance, handling the economic externalities associated with anthropogenic evolution, and controlling novel emerging pathogens such as the SARS virus, Ebola virus, and H5N1 avian influenza virus. At the University of Washington, Dr. Bergstrom teaches undergraduate courses on evolutionary biology, evolutionary game theory, and the importance of evolutionary biology to the fields of medicine and public health.

Lee Alan Dugatkin is a professor and Distinguished University Scholar in the Department of Biology at the University of Louisville. His main area of research is the evolution of social behavior. He is currently working on the evolution of cooperation, the evolution of antibiotic resistance, the interaction between genetic and cultural evolution, as well as a number of history of science projects. Dr. Dugatkin is the author of more than 165 articles on evolution and behavior in journals such as *Nature* and the *Proceedings of the National Academy of Sciences of the United States of America* and of several trade monographs on the evolution of cooperation and on the history of science. He is also the author of *Principles of Animal Behavior*, Third Edition.

PREFACE

What a time it is to be an evolutionary biologist! In the first edition of this book, we wrote that we envy the student taking a class in evolutionary biology today. Recent events only strengthen this sentiment. For example, since the first edition of the book was released, our understanding of human evolutionary history has been upended by findings including definitive evidence of substantial interbreeding between humans and other *Homo* species such as Neanderthals and Denisovans. Or to provide another example, as the final drafts of this edition were being completed, extensive evidence of a new hominin species, *Homo naledi*, was uncovered in a South African cave. We scrambled to tell its remarkable story before the book went to press. These findings, along with other major advances in our understanding of human evolutionary history, stimulated us to expand our coverage of human evolution from a short section in our first edition to an entirely new chapter in this second edition.

Evolutionary biologists continue to collaborate in new and dynamic ways with researchers in many disciplines and bring to such collaboration a diverse set of perspectives—from areas such as phylogenetics, population genetics, the study of adaptation, molecular genetics, and developmental biology, to name just a few. The result is a much deeper understanding of the history and diversity of life on Earth over the past 4 billion years or so. Our job as the authors of this book is to capture the exciting work that has gone into this effort and to present it in a rigorous and engaging fashion.

To achieve this goal, we draw on our dual roles as researchers in and teachers of evolutionary biology. We each run active labs abuzz with the excitement that surrounds the science of evolution. We both lecture about evolution to students at our own universities and to audiences around the world. And we are each enthusiasts about the history of science in general and the history of evolutionary biology in particular. The successful strategies we've developed for communicating with these diverse audiences have informed the tone, emphases, and features in this textbook in a way that we hope will excite the scientific imaginations of students and instructors alike.

We relish the fact that *all science* is about testing hypotheses. Hypothesis-driven science has proved to be the most powerful approach ever devised for understanding the nature of the physical world we live in. No other approach even comes close. We convey this through the abundant use of examples in which evolutionary biologists generate and test hypotheses. In this second edition, we continue the path we took in the first edition and include the newest work from around the globe. Through these examples, students will gain an intimate understanding that evolutionary biology is a continually developing field in which theoretical ideas translate into testable predictions and in which the process of hypothesis testing leads to refinements of theory. Through the lens of current research, students can see how the scientific understanding of evolutionary biology is ever changing and that built into science is a system that allows each assumption to be challenged and refined or even rejected based on a preponderance of evidence.

We understand that it is *stories*, not catalogs of facts, that resonate with students (or anyone else). And so, in each chapter, we make use of the natural human inclination to acquire and process information in narrative form. Within the field of evolutionary biology are fascinating stories on many levels: stories of individual scientists and how they came to their discoveries, stories of how human thought has changed over the centuries, stories of how major evolutionary innovations arose in the history of life, stories of how individual species have changed over millennia through biological evolution or, as in the case of many microbes, how a population can change dramatically in a matter of weeks.

Science is much more than narrative, of course. As in all mature sciences, models play a fundamental role in evolutionary biology today. In this book, we devote considerable attention to simple conceptual models of evolutionary processes. Often, such models can be profitably expressed through the language of mathematics, and one of our principal aims in the text is to help students become comfortable with this approach. One of the most important things that students learn in college-level physics or economics classes is how to formulate questions about the real world in the language of mathematical models and how to answer these questions appropriately using mathematical analysis. We believe strongly that this should be a critical component of a college education in the biological sciences as well. At the same time, we recognize that students enter this course with varying degrees of mathematical preparedness, and so we have placed the more advanced concepts in boxes in an effort to offer instructors maximum flexibility in integrating mathematical models into their course.

So that students will gain a firm understanding of the essential foundations of evolutionary reasoning, we introduce several fundamental components of evolutionary thought in Chapter 1 and emphasize them throughout this textbook. These include:

- **Phylogenetics**. All living things on the planet today—and indeed all life that has ever existed—are linked by a shared evolutionary history that evolutionary biologists represent using phylogenetic trees. Thus, to understand evolutionary relationships, whether between two HIV strains or among the different domains of life, students must learn to think in terms of phylogenetic relationships. We consider it crucial that any textbook on evolution seamlessly integrates phylogenetic thinking throughout, and we have done so here. If students walk away remembering just one thing about this book—though of course we hope they walk away remembering much more—it will be the importance of phylogenetic thinking.
- **Population thinking**. Evolutionary change occurs in populations, but most contemporary biology curricula train students to think at the level of the individual, as one would in a physiology course, for example. In this book, we demonstrate how to think at the population level as well, paying careful attention to the properties of populations: population composition, variation among individuals within and between populations, change in the properties of a population over time, and so forth. This population-level perspective, particularly as it relates to the process of natural selection, permeates this book. Because we know that some students initially struggle to master this type of population-level thinking, we devote considerable space to teaching this skill.
- **Natural selection**. Evolution is often defined as "descent with modification." As a population geneticist (CTB) and a behavioral evolutionary biologist (LAD), we both study the processes responsible for such "modification." We convey the importance of this topic to students by teaching them how the process of natural selection has shaped the diversity of life on this planet and how other processes—most notably genetic drift—have also contributed to the myriad forms of life around us.

Features

This textbook integrates the big themes in evolutionary biology—phylogenetics and population thinking—in a way that is both current and accessible. Extensive, in-depth, current research examples, an emphasis on problem solving, and a stunning art program engage students, helping them understand fundamental concepts and processes. Major features include:

- Extensive coverage of **phylogenetics**, which is introduced in Chapter 1 through the examination of a few engaging examples that demonstrate the power of phylogenetic thinking. Soon after, in Chapter 4, Phylogeny and Evolutionary History, and Chapter 5, Inferring Phylogeny, students are taught how to interpret and then build trees that generate testable hypotheses about evolutionary history and compare the relatedness of living organisms. This strong foundation in phylogenetic reasoning is then integrated into the text and art in virtually every chapter that follows.
- We explore fundamental concepts through the lens of phylogenetics and population thinking and reinforce these concepts using **current research examples**, many of which are drawn from research done in the past decade. From Chapter 3's in-depth examination of Hopi Hoekstra's work on natural selection, phylogeny, cryptic coloration, and the Mc1R and Agouti genes in oldfield mice (*Peromyscus polionotus*), to Chapter 11's coverage of Jack Szostak's work on lipid membranes and reproduction in the earliest cellular life forms, to Chapter 19's story of how genetic evidence of interbreeding between humans and both Neanderthals and Denisovans has radically revised our understanding of our evolutionary history, the excitement of current research is captured throughout.
- Significant coverage of **contemporary topics** such as genomics, evo–devo, molecular evolution, and human evolution, including full chapters on the following subjects: Genome Evolution (Chapter 10), Evolution and Development (Chapter 13), Coevolution (Chapter 18), Human Evolution (Chapter 19), and Evolution and Medicine (Chapter 20).
- An in-depth focus on **a few research studies** in each chapter promotes a more complete understanding of how evolutionary biologists come to understand specific concepts. The examples were carefully chosen to offer a **balance of classic and contemporary studies** that most fully illustrate the concept being discussed.
- A beautiful and information-rich **art program** was carefully developed to promote understanding of key concepts described in the text by both engaging students visually and providing them with just the right amount of detail. The art includes distinctive figures that help students in the following ways:
    1. **Phylogenetic relationships** are made clear through the many phylogenetic trees that appear in virtually every chapter. Many of these trees also include in-figure captions, photographs, and line art that enrich students' understanding of the concept or example.

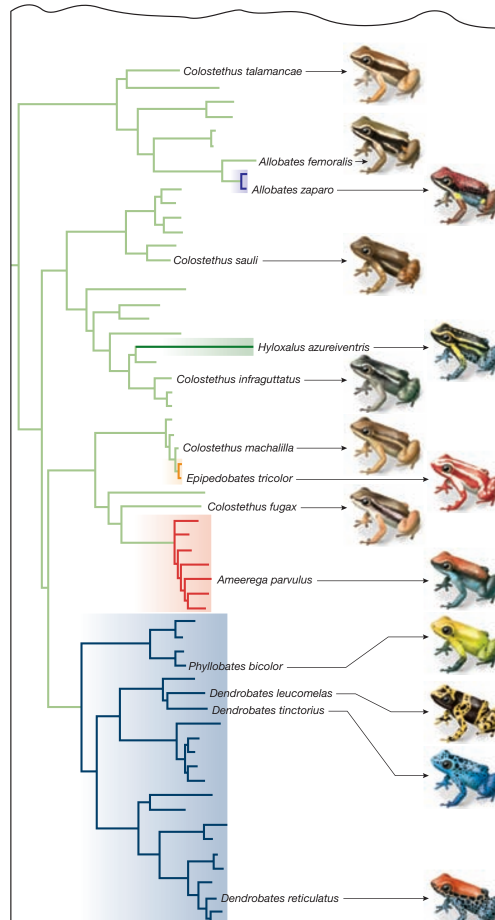

FIGURE 4.24 Convergent evolution in the Dendrobatidae. A phylogeny of the Dendrobatidae with aposematic clades shaded reveals multiple origins of aposematism. Frogs in the left column are cryptic and palatable; frogs in the right column are brightly colored and, with the exception of the mimic *A. zaparo*, toxic. Adapted from Santos et al. (2003), nomenclature following Grant et al. (2006).

2. **Research-style data graphics** are presented much like they appear in the primary literature, but with carefully developed labels and in-figure captions that teach students to interpret and analyze the image or graph visually.

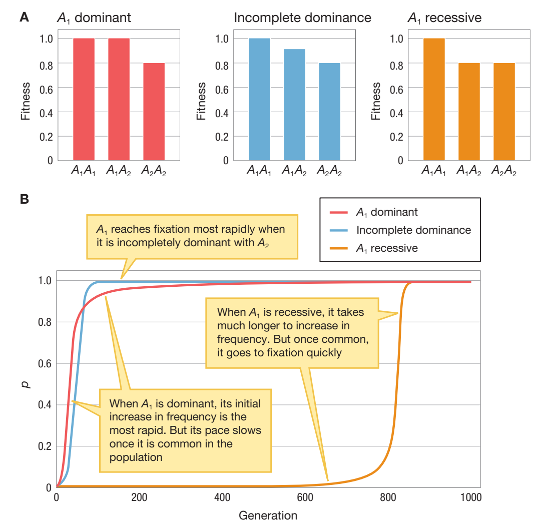

FIGURE 7.13 Directional selection at one locus with two alleles. **(A)** In directional selection, one allele A_1 is favored over another, A_2. This can occur in different ways: A_1 can be dominant (red), A_1 and A_2 can show incomplete dominance (blue), or A_1 can be recessive (orange). **(B)** The trajectories of p, the frequency of the A_1 allele, are illustrated from a starting value of $p = 0.005$.

3. Diagrams of **experimental processes** encourage students to visualize not just the outcome of a research study, but the specifics of how the experiment was constructed so that they can better understand the meaning behind the data.

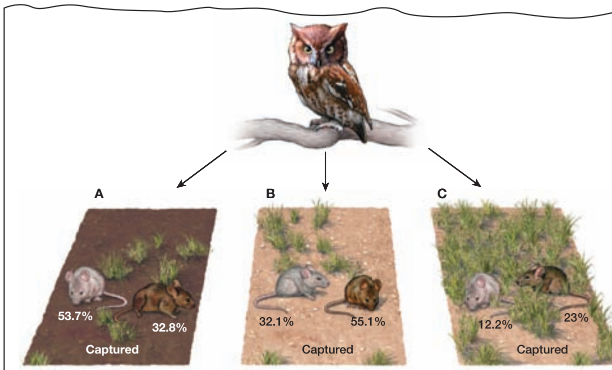

FIGURE 3.9 Early work on predation, coat color, and fitness in the oldfield mouse. Mice with light and dark coats were exposed to owl predators in three different environments: dark background with sparse vegetation **(A)**, light background with sparse vegetation **(B)**, and light background with dense vegetation **(C)**. The identity of the first mouse captured in each trial was recorded. Trials lasted fifteen minutes, and if neither mouse was taken by the owl, the trial ended. The percentages of trials in which mice of a given coat color were the first to be taken by the owl are shown in each panel (percentages in a panel do not sum to 100 because of trials in which neither mouse was taken by the predator). In all cases, owls initially captured a higher percentage of "color-mismatched" mice; namely, those with coat colors that failed to match their environments.

- Clear and accessible coverage of **quantitative methods**, the most difficult of which are in optional boxes. This teaches students how to formulate questions about evolutionary processes and relationships the ways researchers do—in the language of quantitative models.
- High-quality **problem sets** in the end-of-chapter material provide students with extensive practice in formulating and solving problems.

Resources for Instructors

Downloadable Instructor's Resources

These include content for use both in the classroom and online:

- Book art in JPEG and PowerPoint formats.
- Free, customizable Coursepacks, which are accessible directly through instructors' learning management systems and include new adaptive learning modules on interpreting data, phylogenetic trees, and population genetics.
- Test Bank in Examview, Word RTF, and PDF formats.
- Instructor's Manual in PDF format.

For more information and to view samples, go to **wwnorton.com/instructors**.

Test Bank

The Test Bank has been developed using the Norton Assessment Guidelines and provides a quality bank of 1000 items consisting of multiple choice and short answer/essay questions. Each question in the Test Bank is classified by Bloom's taxonomy, learning objective, section, and difficulty, making it easy to construct tests and quizzes that are meaningful and diagnostic.

Instructor's Manual

This helpful online resource for instructors consists of detailed chapter outlines, guides to key readings in the text, and answers to the key concept questions for every chapter. The manual also includes brief guides to accessing and using online simulations, including EvoBeaker.

Coursepacks

At no cost to instructors or students, Norton Coursepacks offer a variety of review activities and assessment materials for instructors who use Blackboard and other learning management systems. With a simple download from our instructor's website, an adopter can bring high-quality digital media into a new or existing online course (with no additional student passwords or logins required). In addition to chapter-based quizzes with art, flashcards, and animations, the Coursepack includes three adaptive InQuizitive modules that develop the core foundational skills students need to do well in the course. The modules, on interpreting data, phylogenetic trees, and population genetics, were written by Christine Andrews, Senior Lecturer at the University of Chicago.

Resources for Students

InQuizitive Learning Modules

InQuizitive is a formative, adaptive quizzing tool that provides a personalized learning experience tailored to each student's learning needs. These free learning modules, accessible directly in the Coursepack, help students hone their understanding outside of class on three key concepts—data interpretation, phylogenetic trees, and population genetics—so that they come to the lectures better prepared. Each module personalizes the quizzing, so students get reinforced practice in the specific areas they need help with most. Instructors can easily review individual and overall class performance data.

Ebook

An affordable and convenient alternative to the print book, the Norton ebook retains the content and design of the print book and allows students to highlight and take notes with ease, print chapters as needed, search the text, and more.

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To the reader: Thank you as well! We greatly appreciate your consideration and selection of this book as your introduction to evolutionary biology. We welcome your comments.

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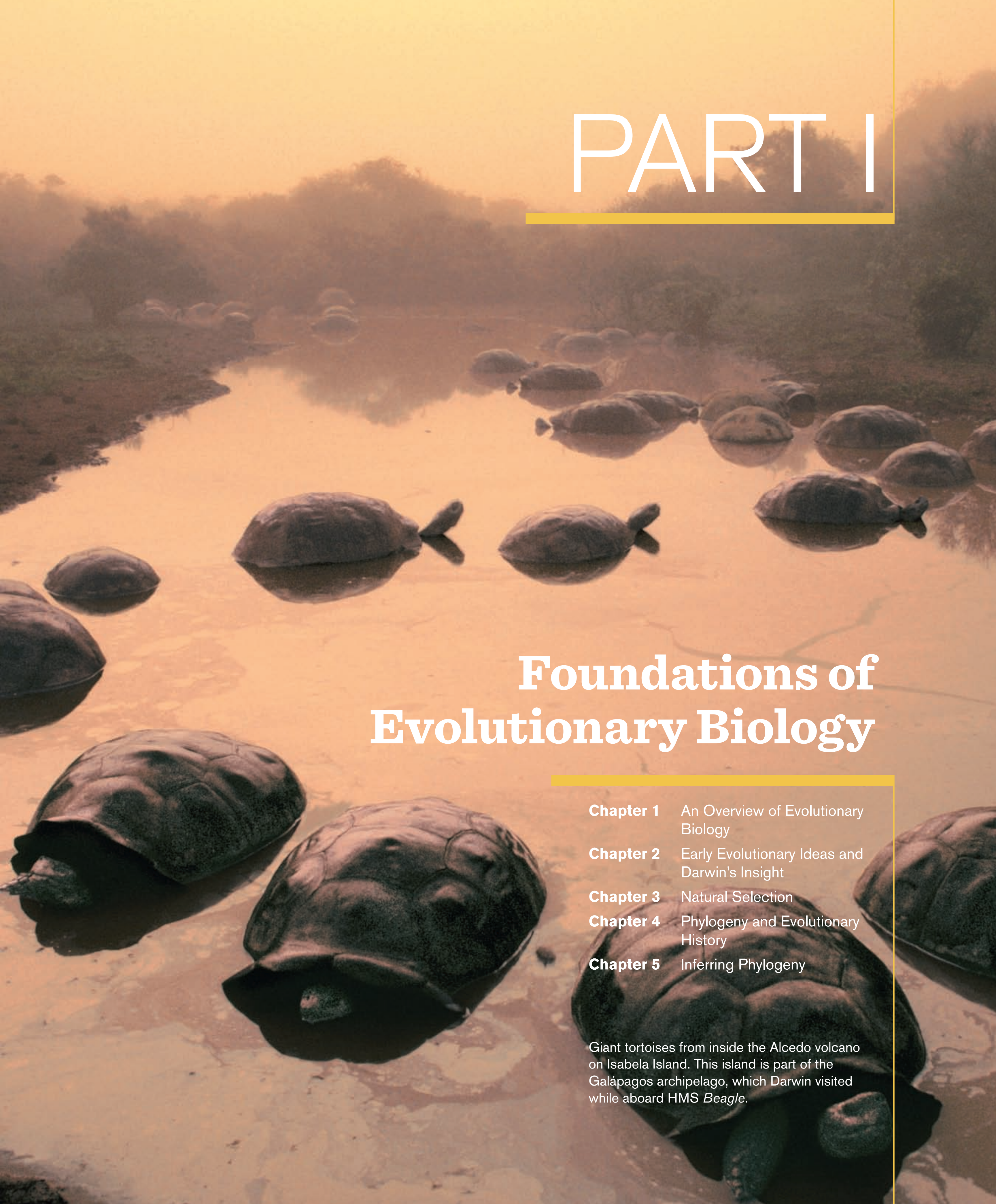

PART I

Foundations of Evolutionary Biology

Giant tortoises from inside the Alcedo volcano on Isabela Island. This island is part of the Galápagos archipelago, which Darwin visited while aboard HMS *Beagle*.

1

An Overview of Evolutionary Biology

◀ The carnivorous dusky pitcher plant (*Nepenthes fusca*) of Borneo traps insects in a liquid reservoir at the bottom of its pitcher.

In his classic book, *The Structure of Scientific Revolutions*, philosopher and historian of science Thomas Kuhn argued that major advances in science are rare, and that true scientific revolutions involve not simply the accumulation of new facts and theories but fundamental changes in the way we think (Kuhn 1962). Once such a revolution takes place, the world is never seen or understood in the same way. When early astronomers and physicists demonstrated that Earth was not at the center of the universe, what Kuhn described as a *paradigm shift* occurred. The very way we thought of Earth and our place in nature fundamentally changed. A similarly dramatic paradigm shift occurred when Charles Darwin laid out his theory of evolution.

In *On the Origin of Species*, published in 1859, Darwin presented two revolutionary ideas. Each had been suggested independently by others before, but never had they been brought together with the conceptual brilliance and the naturalist's eye of Charles Darwin (Chapter 2). First, after decades of observations, collecting data from near and far, reading incessantly, and synthesizing and resynthesizing theories from a number of different disciplines, Darwin recognized that the diversity of life we see around us has descended from previously existing species, which share a common ancestor from further back in time. Second, Darwin realized that the often exquisite fit of species to their environments is primarily a result of **natural selection**, a gradual process in which forms that are better suited to their environments increase in frequency in a population over sufficiently long periods of time. As we will see throughout this book, "sufficiently long" can range from a matter of days to tens of thousands of years, depending on the strength of natural selection and the rate of reproduction of the organisms we are studying. Together, these two ideas proposed by Darwin suggest that the entire organic world—much of everything we see, feel, smell, taste, and touch—is the result of evolutionary changes that have taken place over time.

Once the theory of evolution by natural selection was developed, scientists had at their disposal a natural—as opposed to a supernatural—explanation for the diversity of life on the planet, as well as an explanation for why the vast majority of life-forms that have ever existed are now extinct. More than that, they had a theory that could be used to explain the similarities and differences among all the creatures on Earth and to explain why organisms are usually so well suited to the environments in which they live.

Paradigm shifts have wide-ranging effects, and that was certainly the case for Darwin's theory—so much so that the renowned geneticist Theodosius Dobzhansky wrote, "nothing in biology makes sense except in the light of evolution" (Dobzhansky 1973, p. 125). Without evolutionary theory, biology is composed of a large number of important but disparate subdisciplines. With evolution as its theoretical and conceptual foundation, the biological sciences share a common framework that allows us to understand both the commonalities and differences among living forms; it allows us to make sense of the way that living things function now and to understand how they came to be.

The study of physics is fundamental to understanding our universe, because it allows us to reconstruct the grand story of how the universe came to be as it is, and it lets us understand how the universe operates today. The study of evolution is similarly fundamental in that it allows us to reconstruct the grand story of how all living things came to be and how they (and we) function.

As you will see as you work your way through this book, the characteristics of the organisms you are studying have been shaped by evolutionary processes. Whether you are interested in anatomy, physiology, behavior, molecular biology, genetics, development, medicine, or any other area of biology, a solid understanding of evolution is indispensable.

In this chapter, we will

- Provide a brief introduction to evolution and natural selection, including examples related to (1) artificial selection, (2) antibiotic resistance, (3) conservation biology, and (4) molecular genetics, evolution, and behavior in primates.
- Give an overview of empirical and theoretical approaches to the study of evolution.
- Discuss a more detailed example of the way that empirical and theoretical approaches interact by looking at the evolution of sex ratios.

1.1 A Brief Introduction to Evolution, Natural Selection, and Phylogenetics

The science of evolutionary biology reads like a thrilling detective story in the sense that it unravels a great mystery. Indeed, evolutionary biologists *are* detectives—as are all scientists—but they are much more than that. The study of evolutionary biology allows us not only to infer the relationships among all life that has ever lived and to track the diversity of life across vast stretches of time, but also to test hypotheses through a rigorous combination of observation and experimental manipulations. These observations and experiments may involve examining fossils or contemporary organisms; they may use, among other things, anatomical, physiological, hormonal, molecular genetic, developmental, and behavioral data; and they may involve analyzing data from DNA sequences to population composition (**Figure 1.1**).

At its core, evolutionary biology is the study of the origin, maintenance, and diversity of life on Earth over approximately the past 3.5 billion years. To understand the **evolution** of a species fully, we need to know the ancestral species from which it *descended*, and we need to know what sort of *modifications* have occurred along the way. Darwin referred to this entire process as **descent with modification**.

FIGURE 1.1 Sources of data for testing models of evolution. A few examples of the sources of data that evolutionary biologists use to test their hypotheses: **(A)** data from the fossil record, as shown by this fossil ammonite found in Dorset, England; **(B)** behavioral data, as shown by observing the behavior of gelada baboons in Ethiopia; **(C)** morphological data, as shown by this display of wing color patterns on *Bicyclus anynana* butterfly wings; **(D)** embryological data, as shown by the magnetic resonance imaging of developing mouse embryos between day 9.5 and day 19, when the mouse is born; and **(E)** molecular genetic data, as shown by this DNA sequence film.

To understand the evolution of *Homo sapiens,* for example, we need to understand the primate species from which it descended (as well as other species closely related to this ancestral species) and the changes that occurred over the period in which *H. sapiens* evolved. Because those earlier species are no longer present, we often have to infer their properties by comparing the properties of multiple living species. We use the same reasoning if the species in question is the malaria parasite (*Plasmodium falciparum*) or corn (*Zea mays*). That is, we try to discern the ancestral history of the species in question, and, at the same time, we attempt to track the modifications that have occurred in that species. We aim to understand the process of descent with modification.

One of the most important processes responsible for the modifications that occur over time is natural selection. We will discuss natural selection and other evolutionary processes in greater detail in later chapters. For the time being, we can summarize the process of natural selection as follows. Genetic **mutations**, or changes to the DNA sequence, arise continually and change the **phenotype**—the observable, measurable characteristics—of organisms. These mutations can increase fitness, decrease fitness, or have no effect on fitness, where **fitness** is measured in terms of relative survival rates and reproductive success. Many, perhaps most, mutations will disrupt processes that are already fine-tuned, and thus they will have harmful effects on fitness. By analogy, consider tinkering with a computer program. If you randomly change one line of code, chances are that you will break the program entirely, degrade its performance or, at very best, have no effect on the program's function. But some times you will get lucky—your change may actually improve the program's operation. Genetic mutations are similar. Most are deleterious or neutral, but some mutations turn out to be advantageous in the sense that the individuals who carry them may have more surviving offspring than average. Such genetic changes that improve the fitness of individuals will tend to increase in frequency over time.

The result is evolutionary change by natural selection. The accumulation of advantageous genetic changes, amassed over long periods of time, can produce dramatic effects within a population, even to the extent of producing new species, genera, families, and higher taxonomic orders. Indeed, as we will see many times throughout the course of this book, the process of natural selection is fundamental in what are called the **major transitions** that have taken place over the past 3.5 billion years of life on Earth—the evolution of the prokaryotic cell, the evolution of the eukaryotic cell, the evolution of multicellularity, and so on.

Repeatedly throughout this book, we will examine the power of natural selection in shaping the life that we see around us. We begin with some of the practical applications of understanding evolution via natural selection. Then we examine phylogenetics—how evolutionary history can be inferred using patterns of common descent—to again address an issue of practical application, in this case policies in conservation biology. The examples in this section, as well as all the examples we discuss in this chapter, are meant to illustrate some of the major concepts, methods, and tools that biologists use to understand evolution.

Evolutionary Change and the Food We Eat

The next time you sit down for a meal, take a look at the items on your plate. Whether you're enjoying a home-cooked supper or fast-food takeout, the food you are eating is almost certainly the product of evolutionary change due to intense **selective breeding** over time (Denison et al. 2003; Abbo et al. 2012; Larson et al. 2014) (**Figure 1.2**). Indeed, humans have been selectively breeding grains, such

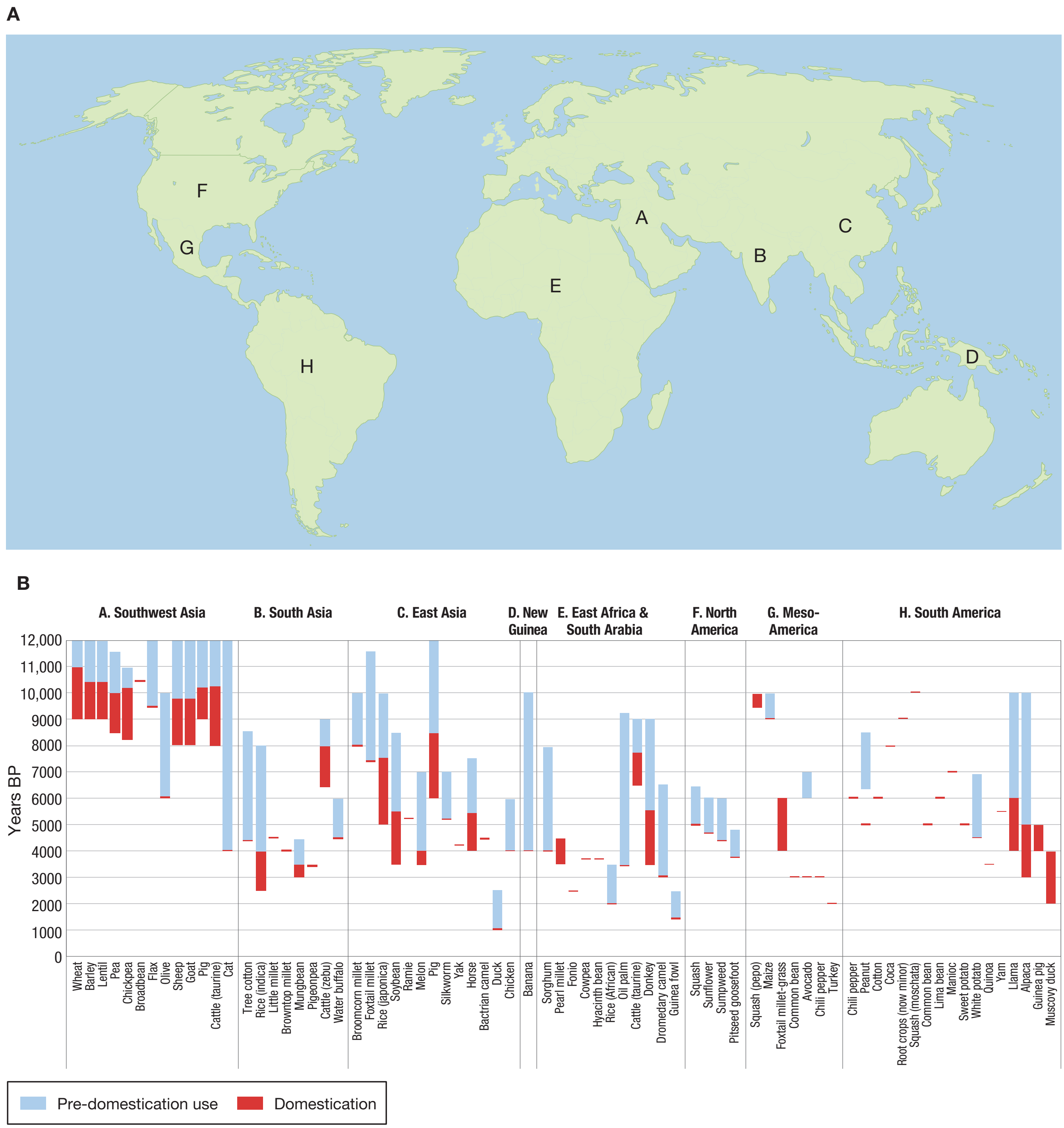

FIGURE 1.2 Domestication of plants and animals around the world. (A) A map showing locations where at least one plant or animal domestication event is thought to have occurred. Labels A–H represent geographic regions seen in panel B. **(B)** A chronology of when and where plants and animals were domesticated. Where possible, extended bars denote the period of pre-domestication use (blue) and the period during which domestication took place (red). Where exact domestication periods are unknown, narrow bars denote the latest possible date of domestication. Adapted from Larson et al. (2014).

as barley (*Hordeum vulgare*) and wheat (*Triticum aestivum*), as well as lentils (*Lens culinaris*) and peas (*Pisum sativum*), for more than 10,000 years (Garrard 1999; Zohary and Hopf 2000; Abbo et al. 2003).

The process of human-directed selective breeding, known as **artificial selection**, is straightforward. In the case of crops, in each generation the best plants—for example, those that are the hardiest, quickest growing, and best tasting—are chosen as the parental stock for the next generation (**Figure 1.3**). If this process is repeated over time, the population of plants increasingly takes on these beneficial characteristics.

Artificial selection by humans is thus a counterpart to natural selection. With natural selection, traits that are associated with increased survival and reproduction increase in frequency. With artificial selection, humans choose which individuals reproduce, and in so doing, we select traits that are in some way beneficial to us. Such selective breeding can produce dramatic results. For example, the productivity of wheat (*Triticum aestivum*), rice (*Oryza sativa*), and corn (*Zea mays*) has doubled since 1930; much of that increase is due to selection for genetic crop strains better adapted to their agricultural environments (Jennings and de Jesus 1968; Ortiz-Monasterio et al. 1997; Duvick and Cassmann 1999). And the same holds true when we look at the selective breeding of animals, which has resulted in increased egg production by chickens and increased milk production by dairy cows (Tixier-Boichard et al. 2012; Mancini et al. 2014).

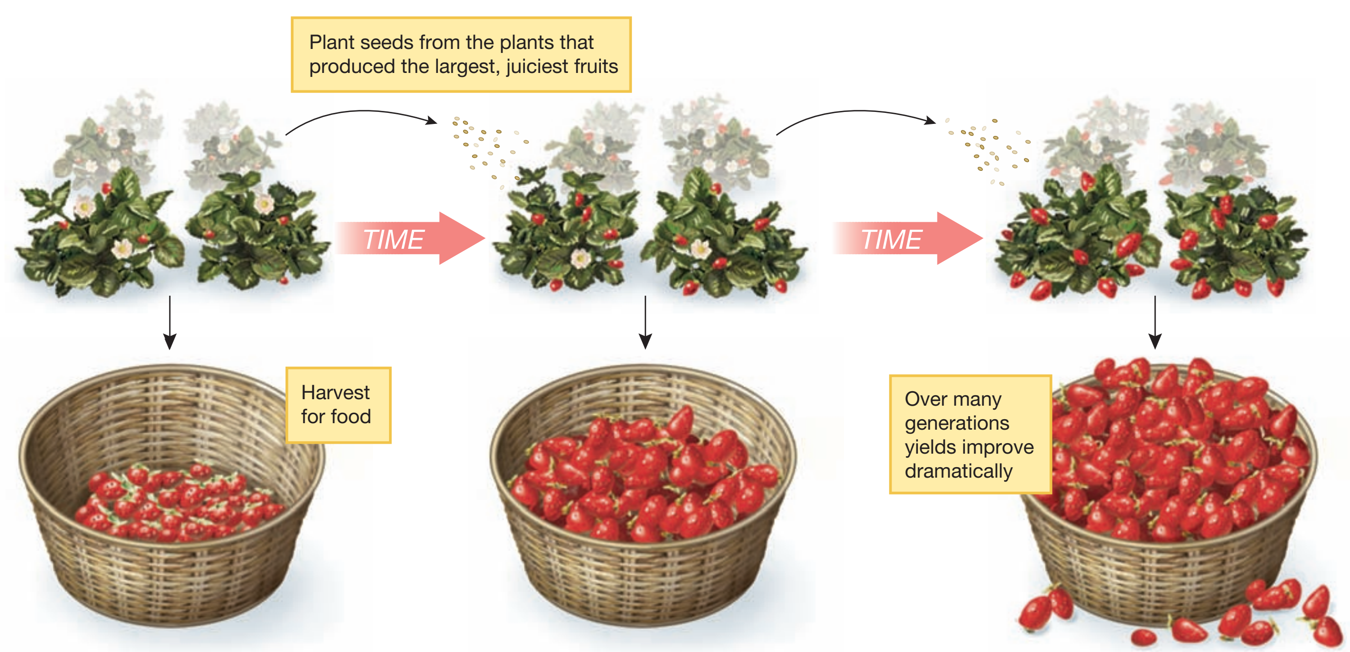

FIGURE 1.3 The process of artificial selection. Darwin used strawberries as an example of artificial selection, writing, "As soon, however, as gardeners picked out individual [strawberry] plants with slightly larger, earlier, or better fruit, and raised seedlings from them, and again picked out the best seedlings and bred from them, then, there appeared (aided by some crossing with distinct species) those many admirable varieties of the strawberry which have been raised during the last thirty or forty years" (Darwin 1859, pp. 41–42).

Even as artificial selection improves the quality and yield of crops and livestock, other evolutionary changes have detrimental effects on the human food supply, as we see with pesticide resistance. Although 10% to 35% of all U.S. crops are still lost to insect damage each year, the development of pesticides was a major breakthrough in reducing crop pests and thereby increasing crop productivity (Pimentel and Lehman 1991; National Research Council 2000). Natural selection, however, will tend to favor crop pests that are most resistant to such pesticides—as occurred when diamondback moths evolved resistance to one of the most frequently used insecticides of the late 1980s—resulting in an "arms race" between pest species that feed on crops and humans determined to get rid of such species (Ceccatti 2009; Furlong et al. 2013). As resistant pests increase in frequency, humans produce ever-stronger insecticides. Because evolutionary change occurs quickly in insects because of their short generation times, humans often lose this particular arms race, and therefore we continually need to develop new pesticides.

Why do we call the evolution of resistance to pesticides natural selection instead of artificial selection, given that humans are the ones producing and distributing the pesticides? The distinction between artificial and natural selection refers not to whether human activity is involved, but rather to whether humans deliberately choose which individuals will reproduce. In the case of increasing grain yields, humans actively select those varieties with higher yield; in the case of increasing pesticide resistance, humans produce the pesticides but do not deliberately choose pesticide-resistant strains of insects for further reproduction. Indeed, what we want—pests easily killed by our pesticides—is just the opposite of what natural selection produces. Desirable or otherwise, evolutionary change due to human activity is sometimes called *anthropogenic evolution* (Carroll et al. 2014).

A problem similar to that of resistance to pesticides unfolds when we look at another product produced by humans: antibiotics.

Evolutionary Change and Pharmaceuticals

One theme that we will return to repeatedly throughout this book is the manner in which research in evolutionary biology can inform our understanding of disease and help us to design more effective responses to the problems associated with disease. For example, the discovery and development of antibiotic drugs for preventing or treating bacterial infections was one of the major medical developments of the twentieth century. But ever since humans first began using antibiotics, medical practitioners have had to deal with bacteria that are resistant to these drugs. The first modern antibiotic, penicillin, was introduced clinically in 1943; within a single year, penicillin resistance was observed, and within 5 years it had become common in a number of bacterial species. Since then, numerous new antibiotics have been developed and introduced to the market, only to lose their effectiveness within a matter of years as bacteria evolved resistance to the drug (Lacey 1973; Piddock et al. 1998; CDC 2007) (**Figures 1.4** and **1.5**). The evolution of **antibiotic resistance** is the result of natural selection and can be understood only in the context of evolutionary biology.

Bacteria reproduce at an astounding rate—in some cases, as frequently as once every 20 minutes. They reach enormous population sizes—a single gram of feces