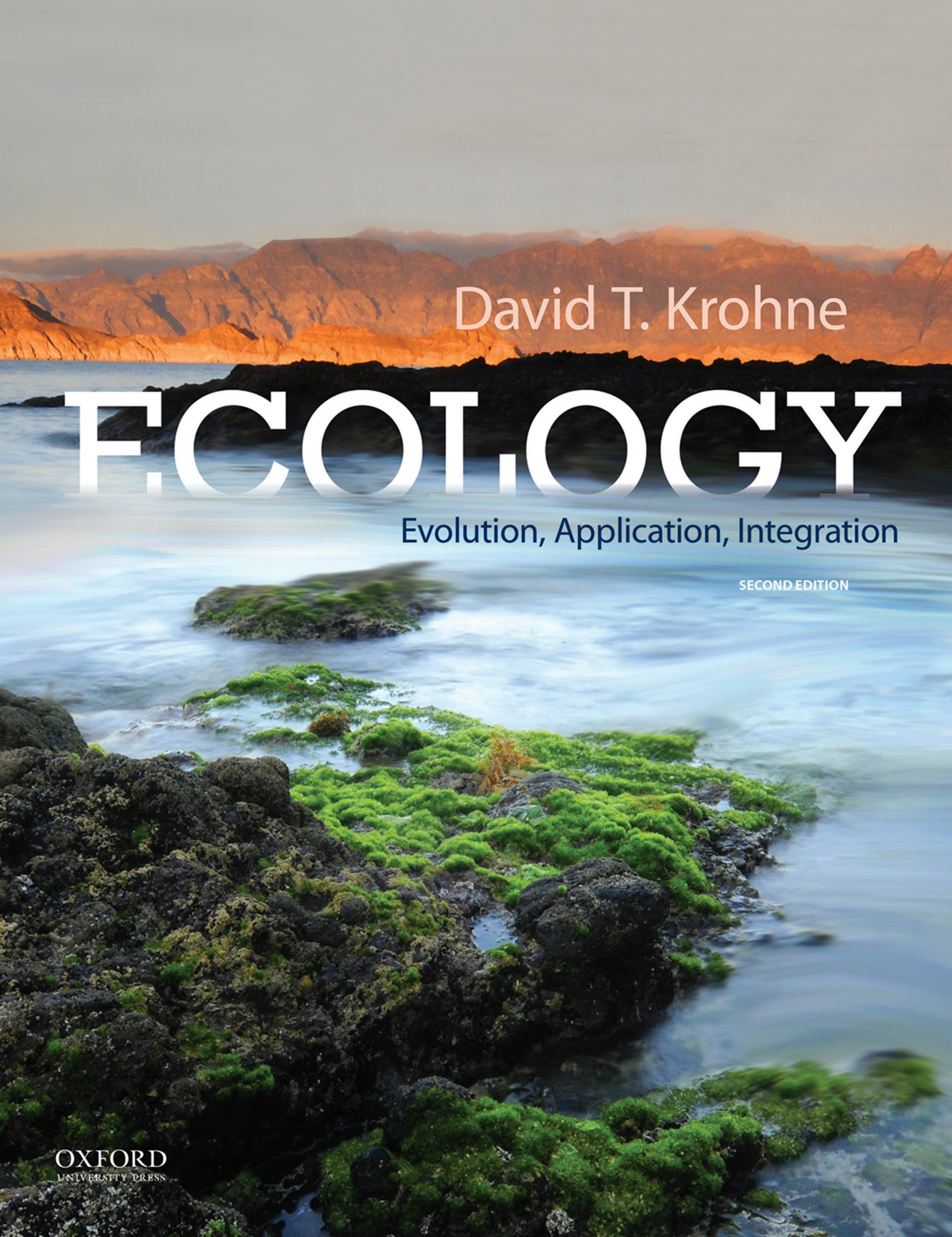

David T. Krohne

ECOLOGY

Evolution, Application, Integration

SECOND EDITION

OXFORD
UNIVERSITY PRESS

Ecology

SECOND
EDITION

Ecology

EVOLUTION, APPLICATION, INTEGRATION

David T. Krohne
Wabash College

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To Dave, Eric, and John

About the Author

David T. Krohne received his BA from Knox College in 1974 and his PhD from the University of California, Berkeley, in 1979. Dr. Krohne was the Norman E. Treves Professor of Biology at Wabash College, where his ecology and evolution courses included field experiences for students in the Everglades, the Florida Keys, the Galápagos, the rainforest, and Yellowstone. In 2003, Dr. Krohne received the McLain-McTurnan-Arnold Excellence in Teaching Award. Dr. Krohne's research interests include the ecology and genetics of populations of small mammals, the population dynamics and conservation biology of rare prairie plants, the structure and organization of tallgrass prairie plant communities, and a 25-year rephotography study of the Yellowstone fires of 1988. He retired from Wabash College in 2010.

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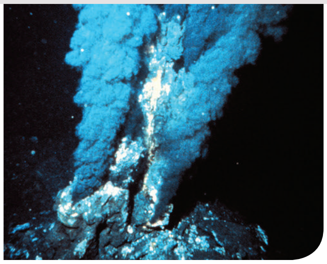

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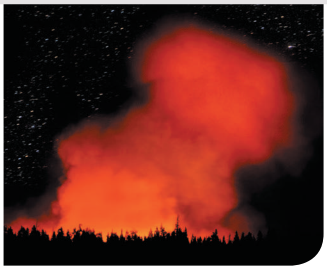

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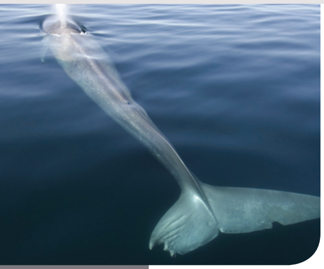

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Preface

The natural world—the Earth and its myriad plant and animal communities—is inherently interesting to many students. Ecology, the scientific analysis of these systems, is a fascinating but dauntingly complex collection of interactions. The sheer volume of information, terms, and principles can be overwhelming for a student confronting it all for the first time. This is especially true given that the vast majority of the students taking ecology courses come from a wide range of life science majors. Many students rightfully wonder, "Why is learning ecology important to me?" Therefore, my goal has been to provide an approach that transforms ecology from a collection of loosely associated pieces of information into an integrated, concept-driven, and comprehensible system of understanding. I do this while also shedding light on the impact humans have on ecosystems. To accomplish this, the text presents ecological theory and applications within an evolutionary context. Importantly, the text also develops scientific reasoning skills by teaching students not just what we know about the field, but how we know what we know.

More Evolution

This text *integrates modern evolutionary theory throughout*. Why is evolution pedagogically valuable? Evolution has great explanatory power—most ecological interactions are rooted in adaptive evolution. Moreover, as students learn to place ecological problems in an evolutionary context, they find they can memorize less because they are able to deduce key ideas. Once they have seen the process of adaptive evolution in one context, they can anticipate its role in the next, replacing rote learning with insight and logic. In every chapter, both through integrated textual discussions and also the "The Evolution Connection" boxes, I direct students' attention to the reciprocal relationship between ecology and evolution, highlighting that evolution is driven by ecology and ecology is driven by evolution and the organism's adaptations. Chapter 14, for example, The Structure of Communities, not only discusses "community heritability and structure" in a box called The Evolution Connection but also explores other aspects of evolution and adaptation throughout the chapter, such as the effect of coevolution on community structure, and how analysis of the genetic relationships among related species influences their ability to coexist.

More Application

The audience for general ecology courses is made up of a wide array of life science majors, ranging from future ecologists to premedical and health majors. Students learn more effectively when the topic of study has relevance to their experience. This text addresses the needs of this diverse set of majors by introducing engaging, real-world examples, especially those that examine the relationship between ecology and its application in the form of environmental science. In addition to chapter-opening questions and stories, and full chapters on subjects such as conservation biology (Chapter 19) and human global ecology (Chapter 21), all chapters include "The Human Impact" boxes, which highlight important environmental issues. Importantly, the text continually asks the student to think critically and quantitatively within these applied contexts; therefore, quantitative topics are presented within the context of real-world applications and examples. Examples of such discussions are woven throughout the text, touching on such topics as human-induced evolution as a result of insect pesticides (Chapter 2);

changes to coral reefs ("The Human Impact," Chapter 3); competition from invasive species transported by people ("The Human Impact," Chapter 13), and the way in which forest roads can prevent the normal movement patterns of forest species such as monkeys (Chapter 18).

More Process of Science

To train students not only in what we know about ecology but also how we know what we know about the subject, the text employs a question-based pedagogy. Each chapter begins with a fundamental ecological question. The sections of the chapter are designed around a logical sequence of smaller questions, the answers to which eventually enable the student to answer the chapter's main question. This approach models the process of science—researchers address fundamental ecological questions in the same way. As students gain experience with this approach, they can apply it to new problems and questions. Also, every chapter features "On the Frontline" boxes highlighting recent studies that illustrate the application of the scientific method to the subject of the chapter. In these boxes, the hypotheses and the predictions that follow are clearly presented and the data that support or reject those hypotheses are explained. Finally, because developing quantitative insight and problem-solving skills is a core objective for the course, the text presents quantitative topics clearly and within applied contexts. More advanced mathematical elements are isolated and explained in boxes called "Do the Math." Examples include the discussion of population change (Chapter 8) and ways to measure the relative contributions of the environment and genetics in behavior (Chapter 6).

Teaching and Learning Features

- **"The Evolution Connection" boxes:** Some relevant evolutionary principles require supplementary discussion. These boxes illuminate additional evolutionary concepts that apply to the ecological content of the chapter.
- **"The Human Impact" boxes:** These boxes apply important principles from the chapter to significant environmental issues.
- **"On the Frontline" boxes:** These boxes highlight a recent study that illustrates the application of the scientific method to the subject of the chapter. The hypotheses and the predictions that follow are clearly presented, and the data that support or reject these hypotheses are explained.
- **"Do the Math" boxes:** Ecology is a quantitative science. These boxes supplement the chapter by explaining additional quantitative topics and equations, giving the student an opportunity to focus on the mathematics at the heart of ecological study.
- **Active learning features:** Students are encouraged to engage in reading through several question-based features. "Thinking About Ecology" questions, found throughout the chapters, ask students to apply their understanding of key concepts. "The Evolution Connection" and "The Human Impact" boxes conclude with probing queries. Importantly, most figures also include an interpretive question to help the student apply visual data.

New to the Second Edition

This edition of *Ecology* has been thoroughly updated and expanded in ways that adopters suggested would be meaningful. I've incorporated the wisdom and feedback of many faculty around the country and encourage instructors (and students!) to continue the conversations about ecology initiated by the first edition.

Changes of Note

- **Thorough updating.** Every chapter has been thoroughly reviewed and updated. You will find many new studies in the body of the text, keeping the science up to date and current. Overall, 62 percent of the research cited in the text is from scientific studies published since 2006. For example, in Chapter 6, new views on models for sexual selection in insects are offered in the "On the Frontline" feature (2014). Chapter 12 includes new findings regarding the relationship between wolf predation and livestock (2014, see "The Human Impact" box). In Chapter 9, a view from 2014 on the biological control of pests is examined in "The Human Impact" box. Examples like these occur throughout the chapters.
- **More process of science and data analysis.** Eleven of the book's popular "On the Frontline" boxes have been revised and replaced for the purpose of adding currency since the previous edition. Much of the cited research has taken place within the last three years, representing the leading edge of current thinking in the field. Among the material explored is work from Britain that tries to ascertain whether global warming or habitat loss is responsible for the disappearance of boreal plants (Hill and Preston, 2015, Chapter 21); the relationship between forest regeneration and conversion of land for agricultural use (Zermeño-Hernández, 2015, Chapter 20); the extinction debt in myrtle, a Mediterranean shrub whose habitat is experiencing habitat loss, fragmentation, and disturbance (González-Varo, 2015, Chapter 19); the roles of productivity and ecosystem size in determining food chain length in tropical terrestrial ecosystems (Young et al., 2013, Chapter 17); and many other important and timely issues in ecology.
- **New chapter on mutualism.** Users of the first edition told us they would like to see our coverage of mutualism expanded. Thus, we separated mutualism out into its own chapter. This allowed us to provide a more detailed explanation of the foundations of mutualism, explain how it evolves, and describe its ecological consequences. In addition, having three new feature boxes and providing many more examples of mutualistic interactions, the reader is given a comprehensive view of these ecological relationships between two species.
- **Expanded treatment of aquatic systems.** We reorganized the material on aquatic systems (Chapter 5) to present it in a unified, visual format analogous to the treatment of biomes in Chapter 4.
- **Completely revised graph program with even greater emphasis on data analysis.** An improved figure program makes the interpretation of data graphs and charts easier. Each chart is presented using a three-level approach. **Level 1** comprises *one or more summary comments* integrated into the figures with pointers, aimed at highlighting the overall purpose of a graphic; **Level 2** comprises *the caption itself*, providing additional detail; and **Level 3** comprises the *Analyze question* at the conclusion of the caption, a tool that encourages deeper interpretation of a figure.
- **Beautiful new illustrations.** Overall, the art program for the book has been reviewed and clarified in many cases, with more than 160 new figures, including the individual pictorial profiles of aquatic systems found in Chapter 5, and revisions to dozens of existing figures.

Support Package

Oxford University Press offers a comprehensive ancillary package for instructors who adopt *Ecology: Evolution, Application, Integration*. For the second edition, we have developed all-new electronic resources including the new "Dashboard" online assessment system, as well as new interactive multi-media modules from the preeminent multimedia developer, SimBio.

- **NEW! Dashboard Online Assessment System.** Dashboard is an online learning and assessment platform tailored to the Krohne textbook. It delivers a simple, informative, and mobile experience for professors and students. It offers quality content and tools to track student progress in an intuitive, web-based learning environment; features a streamlined interface that connects students and instructors with the most important course functions; and simplifies the learning experience to save time and put student progress first. **For more information, go to** www.oup.com/us/dashboard**.** The Krone Dashboard features:
    - Over 1,500 content questions, including 250 multimedia questions—automatically graded in an online gradebook.
    - New auto-graded questions surrounding the FREE Interactive Ecology Simulations suite (found at www.oup.com/us/krohne).
    - Auto-assessed Learning Objectives and course objectives for tracking student's conceptual learning.
    - Interactive Ebook—digital reproduction of the entire textbook featuring multimedia interactivity and easy access to native Dashboard quizzes—lends students a brand-new multi-format learning experience.
    - Online glossary and flashcard activities for drilling new terms.
- **NEW! SimBio Virtual Labs® Modules:** The second edition now comes with the option to include four modules from **SimBio**, leading developers of inquiry-driven teaching tools designed around sophisticated interactive simulations of biological systems. The modules (**Finches and Evolution, How Diseases Spread, Keystone Predator,** and **Isle Royale**) challenge students to think critically as they learn key concepts and discover underlying mechanisms via guided experimentation. Auto-graded quizzes, an easily exportable gradebook, and a variety of supplemental teaching materials make the modules easy to implement while ensuring a positive and successful learning experience for students.

The Ancillary Resource Center (ARC), located at www.oup-arc.com/krohne, contains the following additional teaching tools:

- **Digital Image Library:** Includes electronic files in PowerPoint format of every illustration, graph, photo, figure caption, and table from the text in both labeled and unlabeled versions
- **Lecture Notes:** Editable lecture notes in PowerPoint format for each chapter help make preparing lectures faster and easier than ever. Each chapter's presentation includes a succinct outline of key concepts and featured research studies, and incorporates the graphics from the chapter.
- **FREE Interactive Ecology Simulations:** This edition's digital supplements include ten FREE online simulations demonstrating core quantitative concepts, from Demographic Stochasticity to Poisson Analyses of Dispersion, essential to the contemporary ecological scientist. Freely available at www.oup.com/us/krohne, these simulations are responsive and interactive, mathematically rigorous, and ideal for individual study or live exchanges in the lecture hall—they put ecological analysis at the students' and instructors' fingertips.
- **Computerized Test Bank:** Test item file, written by the author, includes over 500 multiple-choice, fill-in-the-blank, and short-answer questions.

Contact your local OUP sales representative or visit www.oup-arc.com/krohne to learn more and gain access to these instructor resources.

Acknowledgments

A project like this does not come to fruition without the help of many people. I have had the benefit of teaching with colleagues who not only have a deep understanding of science but have devoted their lives to communicating their understanding to students. For this I'm grateful to the Wabash College Biology Department, especially David Polley, John Munford, and Eric Wetzel. Our conversations about teaching shaped not only my own classroom work but the approach I've adopted in this text. I also benefited from my interactions with a generation of students at Wabash College who helped me test the approach and structure of this book. It was from them that I learned the pedagogical value of asking good questions. I thank Greg Hoch for the ongoing conversations that have challenged and deepened my understanding of ecology and evolution. I first learned to appreciate the beauty of ecology and its relationship to evolution from Peter Schramm of Knox College, a gift I cannot repay. I am grateful to the team at Oxford University Press for helping me turn an idea into a book. It was Jason Noe, senior editor, who guided me from a concept to an effective, coherent structure and organization. Thom Holmes, the developmental editor on this project, keenly edited my writing and brought his wisdom and creativity to bear on the pedagogical features in this book. Both were instrumental in shaping this second edition. Associate editor Andrew Heaton somehow managed to keep track of a complex art manuscript and ensure that it meshed with the text. Assistant editor Benjamin Olcott played a vital role in helping to develop the outstanding new program of electronic ancillaries. Development intern Andy Blitzer contributed mightily to the final preparation of the manuscript and vetting of the art manuscript. In production, art director Michele Laseau, production editor Keith Faivre, and the team at Dragonfly Media Group, including Craig Durant, Caitlin Duckwall, and Rob Duckwall, worked together on a tight deadline to turn my manuscript into a visually appealing textbook. I would also like to thank Patrick Lynch, editorial director; John Challice, vice president and publisher; Frank Mortimer, director of marketing; David Jurman, marketing manager; Colleen Rowe, marketing assistant; Marissa Dadiw, advertising and promotions associate, and Bill Marting, national sales manager.

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Part 1

Organisms, the Environment, and Evolution

Horseshoe crabs are one of the most ancient and persistent species we know. They evolved some 450 million years ago, yet they persist today in vast numbers in the shallow seas to which they are adapted. In Part 1 we explore the process of adaptive evolution—the responses of organisms to their physical and biological environments. We will examine the mechanisms of evolution, the basic environments that organisms inhabit, and the ways these environments shape their adaptations. Chapter 6 explores adaptations to members of their own species. In Chapter 7 you will see that intraspecific variation is both a requirement for adaptive evolution and a result of it.

Chapter 1

Introduction to Ecology

CONCEPTS

It is early spring in the Swan Valley in northwest Montana. Much snow remains but scattered patches of bare ground have emerged on south-facing slopes exposed to the sun. A snowshoe hare (*Lepus americanus*) nibbles the buds of a young alder along a creek bottom. The hare, in its pure white winter pelage, stands out against the brown snow-free background (Figure 1.1). Another hare feeds nearby, this one mottled brown and white in transition from its winter to summer coat. One hare is conspicuous; the other is camouflaged.

L. Scott Mills of the University of Montana studies the ecology of snowshoe hares in this valley. By following the fates of animals wearing radio collars, he has found that hare mortality is highest in the spring and fall. In this habitat many predators take hares, including lynx, pine martens, coyotes, wolves, and raptors. Mismatches—brown hares in a white habitat or white hares in a snow-free landscape—may be responsible for the high spring and fall mortality. Mills's research asks fundamental *ecological* questions about this system: *How and why does coat color change in snowshoe hares?*

1.1 What Is Ecology?

What makes the change in coat color in snowshoe hares an *ecological* question? **Ecology** is the study of the interactions between an organism and its biological and physical environment. The fate of hares is determined by their predators, by their coat color, and by the amount and pattern of snow cover. But it is also determined by the distribution of the alders, willows, and the other species hares eat. These plants not only provide food for hares, but they also provide cover and protection from predators. Moreover, they affect the amount of snow that accumulates and the rate at which it melts. The key element of this system is *interaction*, the web of relationships among hares, their predators, their food supply, and the physical environment, including climate and soil (Figure 1.2).

Our definition of ecology cannot possibly convey the richness of the field. That is a task that requires the next 20 chapters. However, we

Figure 1.1 **Snowshoe hares.** Snowshoe hares molt from brown to white in winter. Mismatched hares, white in summer or brown in winter, are probably more conspicuous to predators.

can begin the process by exploring more fully the question of coat color in the snowshoe hare. To do so, we must answer a number of questions (Figure 1.3). The answer to each reveals new interactions. The questions also probe the subject at different levels. For example, the direct effects of external stimuli on the hare's physiology are **proximate factors**, direct or immediate causes. Photoperiod and temperature are proximate factors in this system. Changes in photoperiod, increases in the spring and decreases in the fall, initiate the molt. Abnormally high spring temperatures accelerate the molt; lower temperatures slow it. Another level of inquiry addresses the question: *why* do hares have genetic and physiological mechanisms for color change? The answers to this question are higher order causes known as **ultimate factors**. Ultimate factors often have an evolutionary basis. The evidence we have thus far is consistent with the idea that coat color confers some protection from predation. If predation is an important source of mortality, natural selection should favor hares whose coat color camouflages them from predators.

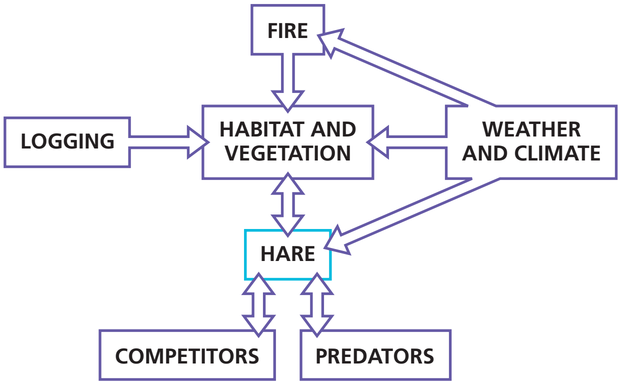
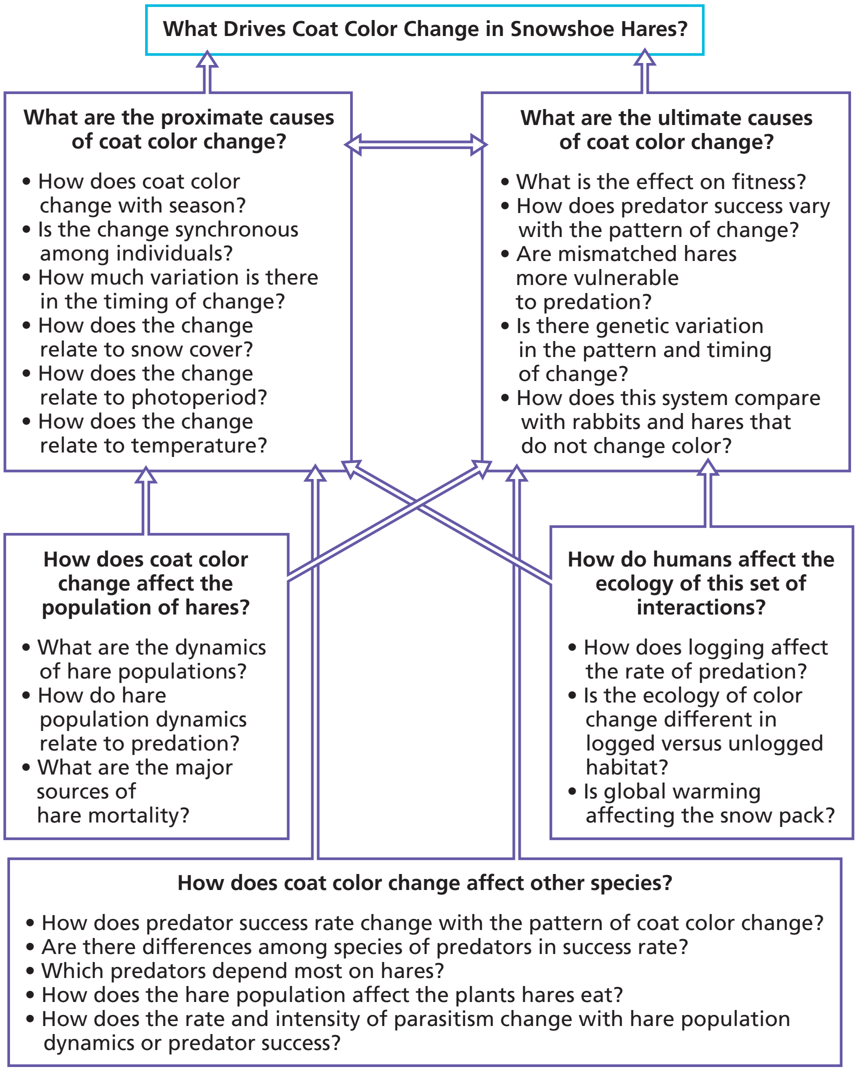


Figure 1.2 **Ecological interactions.** Snowshoe hares are part of a web of ecological interactions that includes humans, other species of plants and animals, and physical factors. **Analyze: What other interactions among components of this system might occur?**

As we work through these questions, we see just how complex the hare's environment really is. The interaction of coat color and predation is just the starting point. We cannot fully understand that relationship in isolation. For example, we know that hares are naturally infected with nematode parasites. The hare's parasite load affects its vulnerability to predation. Also, the parasite load is higher in hares whose nutritional status is compromised. Hares eat the young shoots of aspen, willow, and alder. Fire increases the numbers of these species and their nutrient content. Other herbivores, including animals of vastly different size such as moose and voles, exploit the same plants and thus compete with hares for essential food resources (Figure 1.4). And so the web of interaction grows—to include predation, browsing, parasitism, and competition. Humans too are part of the web. Hare morality is higher in clearcuts than in intact forest because logging removes plant cover that protects hares from predators. Humans affect the system indirectly as well. There is evidence that human industrial activity is causing global warming. As a result, snow arrives later and melts sooner in some places. If this results in more frequent mismatches between hares and their background and thus higher predation, we too play a role in the ecology of coat color in hares.

- **ecology** The study of the interactions between an organism and its biological and physical environment.
- **proximate factor** A direct or immediate cause of a biological process or phenomenon.
- **ultimate factor** The deeper cause of a phenomenon that explains why it occurs.



What Drives Coat Color Change in Snowshoe Hares?

What are the proximate causes of coat color change?

- How does coat color change with season?
- Is the change synchronous among individuals?
- How much variation is there in the timing of change?
- How does the change relate to snow cover?
- How does the change relate to photoperiod?
- How does the change relate to temperature?

What are the ultimate causes of coat color change?

- What is the effect on fitness?
- How does predator success vary with the pattern of change?
- Are mismatched hares more vulnerable to predation?
- Is there genetic variation in the pattern and timing of change?
- How does this system compare with rabbits and hares that do not change color?

How does coat color change affect the population of hares?

- What are the dynamics of hare populations?
- How do hare population dynamics relate to predation?
- What are the major sources of hare mortality?

How do humans affect the ecology of this set of interactions?

- How does logging affect the rate of predation?
- Is the ecology of color change different in logged versus unlogged habitat?
- Is global warming affecting the snow pack?

How does coat color change affect other species?

- How does predator success rate change with the pattern of coat color change?
- Are there differences among species of predators in success rate?
- Which predators depend most on hares?
- How does the hare population affect the plants hares eat?
- How does the rate and intensity of parasitism change with hare population dynamics or predator success?

Figure 1.3 Research questions. Ecological research proceeds by asking a series of specific research questions. In this example, the answer to each of these questions ultimately answers the broader question: What causes coat color change in snowshoe hares?
Analyze: Can you devise an experiment to address one of these questions?

Figure 1.4 Competitors of hares. Other herbivores such as moose (a) and voles (b) compete with hares for food despite the fact that they are of vastly different size.

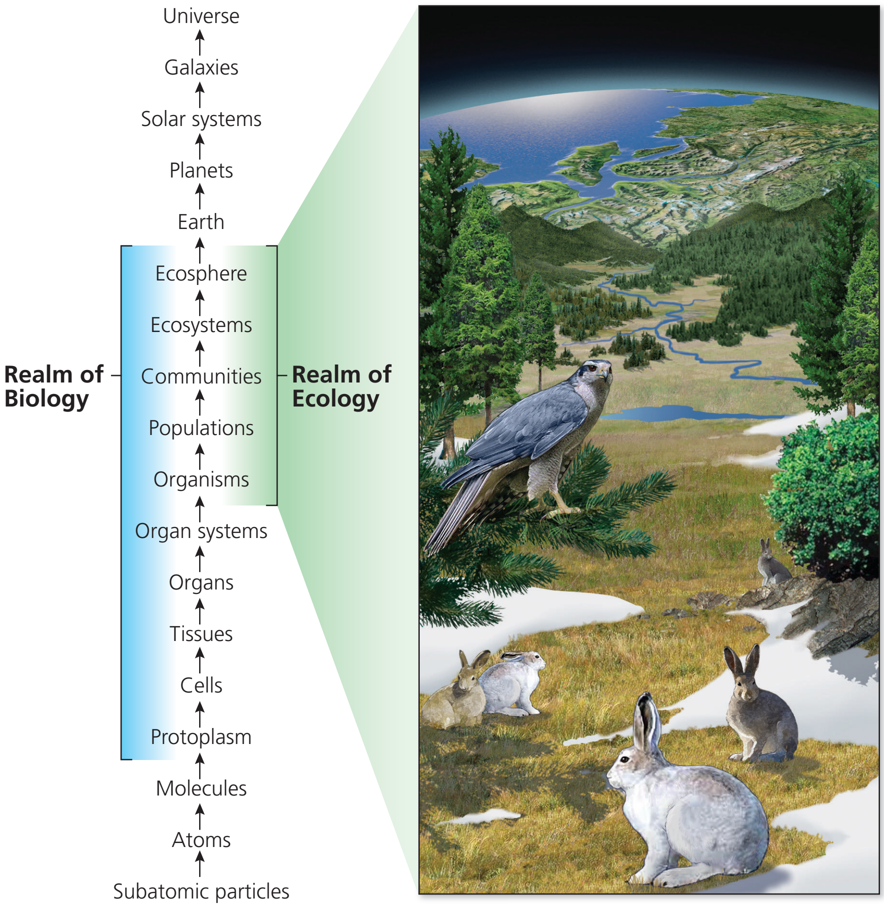


Figure 1.5 **The hierarchy of biological systems.** Biological systems are arranged in a hierarchical organization in which each level is more inclusive than the one below. Often, new properties emerge in the transition from a lower to a higher level. **Analyze: Can you give an example of a property that emerges in this way?**

The ecology of this system encompasses several levels of biological organization. Ecology falls at the upper levels of the traditional hierarchical organization of biological systems (Figure 1.5). The focus of ecology is at the higher, more inclusive levels of this hierarchy. Ecology itself is hierarchically subdivided as well. Some ecologists work at the **organismal level**. They study interactions between individuals and their environment. Physiological ecology and behavioral ecology traditionally address organism-level interactions. **Population ecology** focuses on the dynamics of a group of individuals of a single species. The analysis of the causes of fluctuations in the numbers of hares is an example of a population-level inquiry. Groups of coexisting species constitute an **ecological community**. The hares, their food plants, their predators, parasites, and competitors are part of a community. The next most inclusive level of organization in ecology is the **ecosystem**. The ecosystem is composed of all the interacting living (**biotic**) and nonliving (**abiotic**) components of a community. Abiotic components include the geology, soils, and climate in the ecosystem. The summed ecosystems of the Earth, that is all life and its interactions with the physical environment, constitute the **biosphere** or **ecosphere**.

The example of the hares and the relationships depicted in Figure 1.3 illustrate a fundamental aspect of the conceptual structure of ecology. Ecologists focus on the organism, the physical environment, and the systems of interactions that arise among them. Indeed, these three elements are present in each chapter of the text. However, the relative emphasis on each shifts depending upon the element

- **organismal level** The level of the biological hierarchy in which the focus is on the individual.
- **population ecology** The study of the interactions between a group of individuals of a given species and the environment.
- **ecological community** A group of coexisting species.
- **ecosystem** All the biotic and abiotic components of a community.
- **biotic** Biological factors such as predation or competition.
- **abiotic.** Physical factors such as temperature or pH.
- **biosphere (or ecosphere)** All the ecosystems of the Earth.

under consideration. In Part 1, Organisms, the Environment, and Evolution, we emphasize the direct interaction between the organism and the physical environment. In Part 2, Populations, and Part 3, Communities: The Interactions Among Species, the emphasis shifts to the webs of interactions among populations and species. Part 4, Communities and Ecosystems, addresses ecosystem processes, the most inclusive set of interactions, where we see the intimate interaction between the physical environment and systems of populations and communities. Part 5 focuses on the application of ecological principles to environmental and conservation issues.

Figure 1.6 Resource management sciences. The resource management sciences develop procedures to manage resources like game, fish, and timber. Big game animals like this white-tailed deer are managed to provide sustainable hunting opportunities.

Ecology is connected to a number of other fields. **Natural history** is the observational study of plants and animals in their natural environment. These observations often lead to ecological questions. For example, natural historians described the change in hare coat color long ago. This observation led naturally to the ecological questions—how and why does the change occur? The primary difference between natural history and ecology is that ecology is usually driven by a specific hypothesis. The observation that hares change color led ecologists to speculate on its ultimate causes and to generate hypotheses about its advantages. Careful natural history work, especially meticulous observation, is essential to the study of ecology. The best ecologists are also fine natural historians. Not only do their observations raise new questions, but they also inform the hypotheses and experiments they devise.

There is a close connection between ecology and the related field of **environmental science**, the study of human impact on the environment. Environmental science is an applied science. Its goal is to identify the causes of human environmental impacts, analyze their effects, and devise solutions to them. Of course, ecology is crucial to this analysis. In each chapter, we will examine some of the important applied aspects of the ecological principles we address. By the time you reach Chapter 21 (Human Global Ecology), you will have a firm grasp of the principles and concepts of ecology. With that information in hand, we then further explore the relationship between ecology and environmental science.

The resource management sciences are applied fields that are also closely connected to ecology (Figure 1.6). **Wildlife management** is the science of ensuring the persistence of populations of game and nongame species for hunters and other wildlife enthusiasts. **Forestry**, **range management**, and **fisheries biology** are sciences devoted to managing and husbanding resources important for human use and consumption. These fields use ecological principles and concepts to ensure that human activities such as hunting, grazing, logging, and fishing are sustainable.

- **natural history** Qualitative or observational study of organisms in their natural environment.
- **environmental science** The study of the human impact on the environment.
- **wildlife management** The study of the methods and principles by which we can maintain viable populations of wildlife species.
- **forestry** The study of management practices that ensure the sustainable harvest and ecological health of forests.
- **range management** The study of management practices that ensure the health and viability of grassland habitats used by domestic or wild animals.
- **fisheries biology** The study of management practices that ensure the sustainable harvest and ecological health of fish populations.

KEY CONCEPTS 1.1

- Ecology is the study of the interactions between an organism and its biological and physical environment.
- Ecologists study interactions at multiple levels of organization: the organism, the population, the community, and the ecosystem.
- Natural history observations raise ecological questions and frame hypotheses.
- Other applied fields such as environmental science and the management sciences apply ecological principles to resources important to humans.

QUESTION:

How are the ecology and evolution of snowshoe hares connected?

1.2 What Important Ideas Will Emerge in Your Study of Ecology?

As you progress through the rest of the text, you will find some recurring ideas—concepts that have wide application in ecology. Ecology, like all sciences, is developing at a rapid pace. New data and new analyses constantly modify our understanding of ecological interactions. However, some principles underlie both classic and the most recent studies. They provide a conceptual framework that allows us to make sense of the overwhelming volume of new information ecologists are generating. Two basic types of concepts will emerge: First, you will discover a set of fundamental ecological principles. These represent the overarching themes that unite and explain ecological systems. Second, that set of principles has been elucidated by the specific application of the scientific method to the unique challenges posed by ecological questions.

What Fundamental Themes Will Emerge?

Perhaps the single most important theme in ecology is its intimate connection with the theory of evolution. We devote an entire chapter to evolutionary biology, but you will find the principles of evolution woven into every chapter. Implicit in our discussion of hare coat color change is the idea that the change is an evolutionary **adaptation**. An adaptation is a trait or combination of characteristics of an individual that increases its **evolutionary fitness**, that is, its survival and reproduction. The living and nonliving components of the environment determine which individuals have the highest fitness. In the case of hares, the pattern of snow cover and predators are environmental determinants of a hare's fitness. These two factors (along with many others) constitute **selection pressure** on hares. That is, they determine which hares survive and which die and how many offspring they produce. Those hares with genes that cause them to change color with the season live longer and ultimately produce more offspring.

- **adaptation** A trait that increases an individual's fitness in a specific environment.
- **evolutionary fitness** The survival and reproduction of a particular individual as determined by its characteristics.
- **selection pressure** The environmental factors (biotic and abiotic) that determine fitness.

The hares are also selective agents on the organisms with which they interact. For example, in some parts of the hare's range, especially where hares occur in great numbers, birch trees incorporate phenols in their tissue. These compounds make the trees less palatable to hares, thus protecting them from browsing. Each new adaptation in one species creates new selection pressures on others. The evolution–ecology connection is pervasive and continuous. It encompasses the three key elements of ecology: the organism, the physical environment, and systems of interactions.

A second important theme is that ecological systems do not necessarily achieve equilibrium. In this way, ecology differs from other areas of biology. The difference arises because ecology lies in the upper tier of the biological hierarchy depicted in Figure 1-5. An important change occurs above the level of the individual. Cells, tissues, organs, and individuals exhibit the property of **homeostasis**, regulatory mechanisms that maintain their physiological parameters within narrow limits. An individual whose temperature rises too high or low or whose internal salt balance or pH is too extreme will die. Thus, natural selection favors homeostatic mechanisms that maintain a dynamic equilibrium within fairly narrow bounds. However, this selective force operates at the level of the individual but not at higher levels of organization. Fitness is a property unique to the *individual*. And natural selection determines which *individuals* live or die. Populations and communities do not have fitness, and natural selection does not favor some populations or communities over others. Thus, there is no imperative for homeostasis at the higher levels of the population, community, or ecosystem.

- **homeostasis** Regulatory mechanisms that maintain an organism's physiological parameters within specific limits.

The ecological phenomenon comparable to homeostasis in organisms is known as the "balance of nature." According to this concept, ecological systems achieve an equilibrium state in which the numbers and diversity of organisms and the interactions among them no longer change. Although many factors can disturb this balance, feedback mechanisms ensure that the system returns to equilibrium. The balance of nature was an important principle early in the history of ecology. Ecologists now appreciate that there is no logical imperative for the balance of nature. In addition, empirical studies document that many ecological systems either do not achieve an equilibrium state or it is ephemeral. We now understand that although there are mechanisms that regulate ecological interactions and move the system toward equilibrium, they do not operate in all systems and they can be overwhelmed by random forces. Modern ecologists recognize the importance of both equilibrium and nonequilibrium in ecological processes.

The human impact on the environment and on ecological processes is another important theme that will emerge. As noted earlier, ecology and environmental science are distinct fields. Still, they are intimately connected. The human impact on the environment is so pervasive that virtually no ecological system on Earth is unaffected by human activity. Humans modify two of the main elements of ecology: the organisms and the physical environment. We are responsible for the elimination of some species and the spread of others; we modify the physical environment by altering the climate as well as the chemical composition of the land, water, and atmosphere. As a result, we radically alter many ecological interactions. Today we cannot assume that any ecological process is pristine; all are affected in some way by human activity. Of course, the human connection is also important because we have an inherent interest in our own health, welfare, and quality of life, all of which are affected by the environment.

What Methodologies Are Important in the Study of Ecology?

The concept of the testable hypothesis is central to the process of science in general and ecology in particular. Again, the ecology of coat color in hares illustrates the idea. Professor Mills made two observations: (1) hare mortality is highest in spring and fall, and (2) predation is responsible for many of these deaths. You might conclude that these observations are ultimately driven by predation on mismatched hares. However, this logic generates not a conclusion but a *hypothesis*. The data are consistent with the predation hypothesis, but they do not prove it.

What data would be needed to test the hypothesis? Good hypotheses lead to testable **predictions**. A prediction is an observation or result we expect if our hypothesis is true. A good hypothesis makes specific, logical predictions that can be tested. Moreover, a good hypothesis is **falsifiable**: it must be possible that some data or observation could unequivocally show that the hypothesis is false. In the case of the hares, the predation hypothesis predicts that the excess spring and fall mortality is due to predation on mismatched hares (Figure 1.7). This prediction allows us to potentially falsify the hypothesis. We can test it by measuring the relative numbers of matched and mismatched hares in the population and the rates of predation each experiences. If it turns out that mismatched hares are no more likely to be captured and eaten than camouflaged hares, we reject the predation hypothesis—it has been falsified. On the other hand, if mismatched hares are preyed upon more frequently than matched hares, we accept the hypothesis. Note that although we can reject a hypothesis as false, we cannot definitively prove it to be true. It is always possible that some other unknown factor correctly explains the pattern of hare mortality. We accept as correct those hypotheses that we cannot prove false.

prediction The result or observation we expect if a hypothesis is true.

falsifiable Describes a hypothesis that can be proven incorrect by data or observation.

You will discover that ecologists study a wide range of organisms. The choice of the study system and the organism is not random—and in fact the choice is crucial to the success of the study. What criteria are important in the choice of the study system? Some species are chosen because we know their basic biology and natural history so well. The researcher can address sophisticated questions and hypotheses without investing time and energy collecting basic natural history information. Sticklebacks, anoles, monkey flowers, columbines, Darwin's finches, and voles are examples of model organisms used to address important questions. Sometimes the researcher chooses a species and system because it lends itself to the analysis of a specific question or hypothesis. Thus, Professor Mills chose snowshoe hares to test hypotheses about climate and predation because that system—hares in the Swan Valley—is ideal for his investigation. Some systems are chosen because they are amenable to experimental manipulation. For example, there are

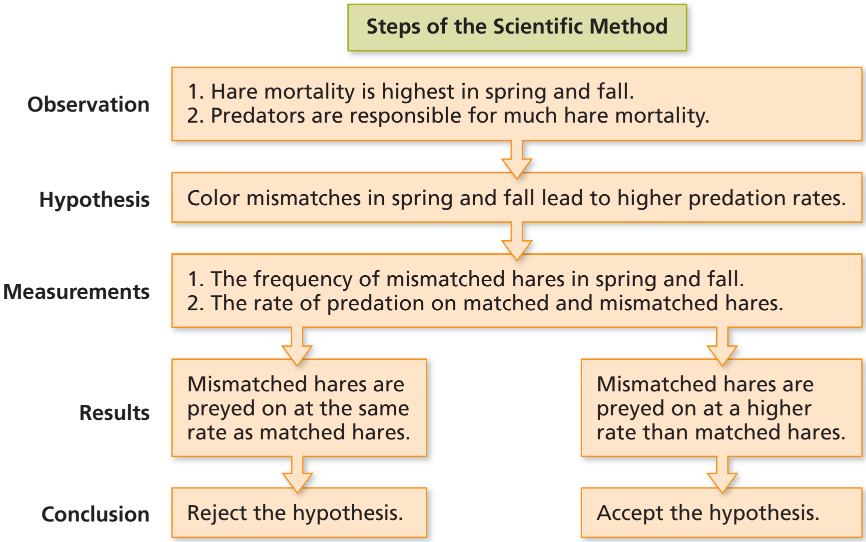


Figure 1.7 Hypotheses. The development of a hypothesis begins with an observation. The hypothesis is tested by collecting data that could potentially show the hypothesis to be false. The results allow the researcher to either accept or reject the hypothesis. **Analyze: If we accept the hypothesis, is it necessarily true?**

many sessile organisms that live on boulders in rocky intertidal marine ecosystems. Researchers can move rocks (and thus organisms) within the system or remove certain species relatively easily. Consequently, the rocky intertidal has been the system of choice in many classic ecological experiments.

This text will also illustrate the importance of mathematics and quantitative analysis in ecology. Mathematics and statistics are especially valuable in larger, more inclusive systems such as populations or communities where the results of experiments are often quantitative. For example, snowshoe hare mortality is greater in the spring and fall. But this pattern is not absolute; mortality does occur at other times. It is the *frequency* of death, a quantitative parameter, which changes over the course of the year. Quantitative results such as these reflect the fact that many causal factors contribute to the ecological variables we measure. Ecology, by its very definition, entails interaction and complex webs of causation. Mathematical analysis allows us to tease apart the relative importance of multiple interacting factors.

Imagine you want to do a set of experiments on competition between hares and voles. You might analyze their competitive interaction by changing the number of voles in the habitat and measuring the population response of the hares. However, in the process you might also alter other interactions in which both hares and voles participate. The effect you measure on the hares is unlikely to be due solely to the direct effect of the experiment; indirect effects also contribute to the outcome. Statistical and mathematical analyses help overcome these obstacles. Figure 1.8 shows a hypothetical example of a graphical analysis that reveals an interaction effect The graph shows that as the number of voles increases, the number of hares declines. The slope of the line quantifies the competitive effect of voles on hares. But notice that the relationship changes with the age of the forest. In both young and old forests, hares decrease when voles are abundant. But the slopes differ with the age of the forest. In other words, there is an interaction between forest age and the effect of voles on the population of hares.

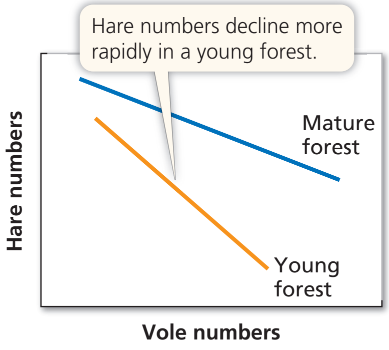


Figure 1.8 Interactions. A hypothetical interaction between the numbers of hares and voles and the age of the forest habitat. When vole numbers increase, hare numbers decline. However, the rate of decline depends on the age of the forest. **Analyze: What would this graph look like if there were no interaction between hares, voles, and the age of the forest?**

Finally, questions we ask about the natural world are crucial to the process of science. The initial study of hare mortality asked, "In which season is hare mortality highest?" The answer suggested another question: "Is the spring-fall mortality increase due to color mismatches?" To answer that question, we must ask if the mortality is due largely to predators or other factors. If the answer to that question is predators, the next question addresses the effect of coat color mismatches on the predation rate.

Our understanding of the natural world progresses as a network of questions, answers, and new questions. The best scientists are skilled at identifying the next logical question. The structure of this text reflects the importance of this skill. Each chapter is organized around a fundamental question such as "How are populations regulated?" or "What is the effect of competition?" Those questions are much too broad to address directly. But if we ask a series of smaller questions, we can begin to develop an answer to the larger question. In this way, our learning reflects the scientific process.

KEY CONCEPTS 1.2

- Three important themes will emerge in your study of ecology:
  - The intimate connection between ecology and evolution.
  - Ecological systems do not necessarily achieve an equilibrium state.
  - Humans have a significant impact on the Earth's ecological systems.
- Ecology employs the scientific method to answer questions about ecological systems.
- Ecology is a quantitative science that relies on mathematical and statistical analyses.
- The questions we ask about the natural world determine the hypotheses we generate and the analyses we perform.

QUESTION:

How does the subject matter of ecology, which lies high in the biological hierarchy, affect the way we study ecological systems?

Summary

1.1 What Is Ecology?

- Ecology is the study of the interaction between an organism and its biotic and abiotic environment.
- Ecology is subdivided into hierarchical categories: the organism, the population, the community, and the ecosystem.
- Ecology is closely connected to natural history, environmental science, and the management sciences.

1.2 What Important Ideas Will Emerge in Your Study of Ecology?

- Ecology and evolution are intimately related.
- Ecological systems do not necessarily exhibit the property of homeostasis.
- Quantitative analysis is an important tool in modern ecology.
- In ecology, as in other fields of science, the questions we ask about nature shape our analyses and experiments.

Key Terms

abiotic p. 6
adaptation p. 8
biosphere p. 6
biotic p. 6
ecological community p. 6
ecology p. 3
ecosphere p. 6
ecosystem p. 6
environmental science p. 7
evolutionary fitness p. 8
falsifiable p. 9
fisheries biology p. 7
forestry p. 7
homeostasis p. 8
natural history p. 7
organismal level p. 6
population ecology p. 6
predictions p. 9
proximate factors p. 4
range management p. 7
selection pressure p. 8
wildlife management p. 7
ultimate factors p. 4

Review Questions

1. Why is ecology so simple to define yet such a deep and rich field?
2. What components of the scientific process are illustrated by the snowshoe hare coat color example?
3. What is the significance of ecology's place in the biological hierarchy?
4. Why are questions so important in science?
5. What do we mean by the term "ecological interaction"?
6. Explain the relationship between ecology and evolution in the snowshoe hare coat color example.
7. What is the relationship between proximate and ultimate causation in ecology and evolution?

Chapter 2

Adaptation and Evolution

CONCEPTS

FEATURES

The Human Impact

On the Frontline

Do the Math

The Evolution Connection

In October 1835 the young naturalist Charles Darwin stood on a rocky shore in the Galápagos and threw a marine iguana (*Amblyrhynchus cristatus*) as far as he could into the sea. It immediately swam back to shore and Darwin repeated the toss. Over and over he threw the iguana into the surf and watched it return to shore: "It invariably returned in a direct line to the spot where I stood. It swam near the bottom, with a graceful and rapid movement, and occasionally aided itself over the uneven ground with its feet" (Darwin, 1839, p. 238).

Although Darwin thought the iguanas ugly ("It is a hideous-looking creature, of a dirty black colour, stupid, and sluggish in its movements"), he was also fascinated by them. He described them in great detail, noting that their tails are flattened sideways and their feet are webbed. In the water their sluggish movements change to graceful undulations that propel them rapidly. He opened the stomachs of several and found them packed with the marine alga *Ulva*. This behavior too interested the young Darwin. Upon returning from a feeding excursion, he noted that they lie on the black lava rock, their bodies oriented for maximum exposure to the sun. Darwin observed that iguanas enter the ocean only reluctantly except to eat. He speculated that this reluctance "may be accounted for by the circumstance that this reptile has no enemy whatsoever on shore, whereas at sea it must often fall a prey to the numerous sharks. Hence, probably, urged by a fixed and hereditary instinct that the shore is its place of safety . . . it there takes refuge" (Darwin, 1839, p. 239).

Darwin was practicing what today we would call *evolutionary ecology*. He was observing the characteristics of the iguana in relation to its environment. Moreover, this work was not based on preserved specimens in a museum; it was conducted in the field, in the iguanas' natural environment. Note too that in his speculation about their reluctance to enter the water he was drawing inferences about the *origin* of their behavior. This hypothesis exemplifies the concept of ultimate causes (Chapter 1).

The set of unique characteristics that Darwin described facilitate iguanas' success in the Galápagos environment. As Darwin noted, its flattened tail and webbed feet—unknown in other iguanas—aid in swimming. We now understand too that its dark color and habit of resting on black lava oriented toward the sun is important in two ways. First, iguanas are poikilotherms; that is, they do not physiologically maintain a constant body temperature, and so their body temperature drops while they are foraging in the cold waters of the Galápagos. Their dark color absorbs rather than reflects sunlight, restoring a higher internal temperature. The iguana's body temperature is also important for digestion. Like many herbivores, iguanas depend on symbiotic bacteria to digest plant matter. Basking maintains a temperature beneficial to their gut bacteria and digestion (Fields et al., 2008).

- **fitness** The ability of an individual to survive and reproduce relative to other individuals in the population.
- **adaptation** A trait that increases an individual's fitness in a specific environment.

The characteristics of an iguana determine its **fitness**, its relative ability to survive and reproduce in the Galápagos environment. Each of these characteristics is an **adaptation**: a trait that improves the fitness of the organism in a specific environment. Darwin's great insight, developed from countless observations, was that adaptations arise over time by an evolutionary process. Moreover, he developed the theory of natural selection as the central mechanism of this evolutionary process. In the example of the marine iguana, we see the intimate connection between evolution and ecology. The adaptations of this reptile evolved in a specific ecological situation: an herbivorous creature inhabiting a set of volcanic islands, nearly devoid of land predators, surrounded by cold marine waters. The evolution of the marine iguana makes little sense except in this ecological context—their evolution and ecology are completely interdependent. And full understanding of the ecology of this species is impossible without understanding the evolution of its adaptive responses to the environment. Thus, we begin this chapter with an evolutionary question crucial to all of ecology: *How do organisms adapt to their environment?*

2.1 How Did Darwin Develop the Theory of Evolution by Natural Selection?

Charles Darwin was invited to join the voyage of the HMS *Beagle* as the ship's naturalist and gentleman companion to the captain, Robert Fitzroy. The *Beagle* was sent on a voyage around the world to improve the maps of many places, especially the coast of South America (see Figure 2.1).

How Did the Voyage of the *Beagle* Change Darwin's Thinking?

The *Beagle* was away from England for five years (Figure 2.2). A number of factors combined to influence Darwin's thinking. First, Darwin was fascinated by

Figure 2.1 The voyage of the HMS *Beagle*, 1831 to 1836. On this voyage Darwin observed the patterns of geographic variation in plants and animals. He was especially intrigued by the unusual fauna of the Galápagos.

geology. Early in the trip he made careful observations of geological features, especially the volcanic Cape Verde Islands in the Atlantic. He began to understand the length of time associated with the origin of volcanic islands in the deep ocean. He carried onboard with him an important contemporary treatise on geology, Charles Lyell's *Principles of Geology*. This book was significant in that it advocated a new view of geology, namely the theory of *uniformitarianism*. According to this view, modern land forms arose slowly by gradual processes rather than by rapid, cataclysmic events. Moreover, observing processes at work today is the key to understanding what occurred in the past. Darwin recognized the application of this concept to the growing science of biology.

Second, Darwin had the opportunity to collect and observe plants and animals across large stretches of the South American continent. As the *Beagle* coasted north along Chile, Peru, and Ecuador, Darwin noticed changes in the organisms—his specimens from different sites along the coast were clearly related but they varied with the geography. Among Darwin's most famous collections were those from the Galápagos Islands, where he made some crucial observations. He noted that many of the plants and animals of the Galápagos are similar to species he had seen on the mainland, yet they were subtly different. In addition, he noted that some groups had diversified into a variety of forms on the islands. The most famous examples are the finches we now know as Darwin's finches (Figure 2.2) and the Galápagos tortoise. Darwin conceived a mechanism to explain the variation in finches and tortoises. He reasoned that an ancestral colonist from the mainland had, over time, diverged into the variants that now occupy each island.

Darwin did not develop the theory of natural selection during the voyage of the *Beagle*. Upon his return to England he spent years studying his collections or the analyses of them done by other experts. He also embarked on a series of extraordinarily detailed studies of organisms, including barnacles, earthworms, and orchids. He opened his first notebook on the subject of evolution in 1837. From this point on, his notes show clearly that he was moving toward the great idea that formed the basis of his classic work, *On the Origin of Species by Means of Natural Selection*.

Figure 2.2 Galápagos finches. Many of the islands of the Galápagos have finches that are unique to that island but are clearly related to those on other islands.

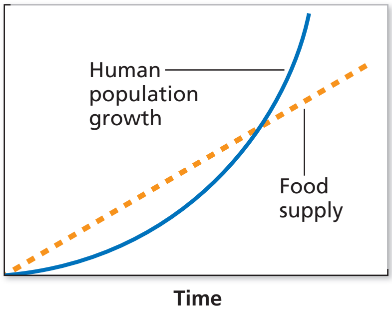
What Was Darwin's Logical Argument?

The observations Darwin made on the voyage of the *Beagle* suggested that evolutionary change had occurred. However, change was not sufficient to advance a theory of evolution. He also required a mechanism. *On the Origin of Species* is an enormously complex and comprehensive treatment of evolutionary change. Nevertheless, Darwin made a simple, cogent argument for his mechanism. It is based on three empirical observations and a logical deduction that follows from them.

First, Darwin documented the wide array of variation within species. His own collections and observations showed that within any species and even within a local population, there are variants—individuals that differ in some way. This was no new insight. Amateur and professional collectors had appreciated it for years. In fact, collectors prized unusual specimens. However, Darwin studied and documented variation more thoroughly and systematically than anyone had before. He also studied the phenomenon in domestic animals. Darwin understood that much of this variation is inherited. In today's terminology, we say it has a genetic basis.

Second, Darwin recognized that most plants and animals have prodigious reproductive potential. He noted, however, virtually no organism achieves its maximum output. External factors reduce the reproductive rate or the survival of the offspring.

Next, Darwin understood the intensity of competition in nature. His thinking was influenced by an essay by the economist Robert Malthus. Malthus argued that there would always be a lower class because human reproduction increases the population exponentially. However, the food supply increases only arithmetically because increases occur only by the addition of new lands to cultivation. Consequently, the human population will inevitably outstrip the food supply (Figure 2.3). Darwin saw evidence of this phenomenon in the natural world. He knew that competition among individuals limits reproduction and survival.



Human population grows faster (exponentially) than the food supply (which grows arithmetically).

Figure 2.3 Food competition. The economist Robert Malthus argued that the human population increases exponentially (solid line), whereas the food supply (dashed line) can only grow arithmetically. Consequently, there will inevitably be competition for food (Malthus, 1798). **Analyze: Where in this graph does competition begin?**

These observations led Darwin to a crucial conclusion: any individual whose inherited characteristics make it more competitive will persist; others will die out. Over time, individuals possessing these advantageous characteristics increase in frequency in a given population relative to others. This is the central tenet of his concept of **natural selection**: individuals with inherited traits that increase their reproductive output or survival will increase in frequency in the population relative to other competing individuals.

natural selection The increase in the frequency of individuals with inherited traits that increase their fitness relative to other individuals.

How Do We View Darwin's Theory Today?

Darwin's insight and his careful work documenting the phenomenon of natural selection place him among the intellectual giants in the history of science. By the middle of the nineteenth century, many scientists already accepted the idea of evolution. Knowledge of the fossil record grew rapidly and geologists suggested older and older ages for the Earth. Darwin's key contribution was a mechanism for evolutionary change that operated on an equally ancient time scale.

One gaping hole in Darwin's idea was the mechanism of inheritance. Darwin devised a theory of blended inheritance in which offspring acquire a mix of characteristics of both parents. It wasn't until the early twentieth century that a valid mechanism of genetics was applied to Darwin's work. Subsequently, biologists united the growing understanding of inheritance with Darwin's mechanism of change. The result, known as the Modern Synthesis, brought evolutionary thinking to the center of the science of biology.

Modern molecular biology has contributed importantly to the development of evolutionary theory. As we will see in this chapter, there are other mechanisms of evolutionary change besides natural selection, but because they depend on an understanding of genetics and molecular biology, Darwin could not have conceived of them. Thus, it is fair to assert that Darwin was correct—but incomplete. The process of natural selection he proposed has been well documented in case after case. But as we shall see, the process of evolutionary change is richer and more complex than Darwin could have imagined.

In the time since Darwin, advances in geology and biology have substantially increased our confidence in the concepts of evolutionary change and the force of natural selection. We have a much more accurate and sophisticated understanding of the age of the Earth and the time span over which evolution has occurred. We also have a vastly more comprehensive history of life from the fossil record that clearly documents the details of change over time. Natural selection itself has been observed in operation in living species and can be inferred from careful analyses of fossils. In sum, the theory of evolution by natural selection has enormous empirical support. Evolution is central to modern biology as both an organizing principle and as a basis for experimental analysis.

KEY CONCEPTS 2.1

- On the voyage of the *Beagle*, Darwin observed and documented geographic patterns of variation within species.
- Three empirical observations (heritable variation with species; high but unrealized reproductive potential; competition for scarce resources) led Darwin to a crucial logical conclusion: those variants that leave more offspring or survive at a higher rate will increase in frequency over time.
- Darwin's theory was correct but incomplete. He did not understand the mechanism of inheritance. And he did not envision other mechanisms of evolutionary change that we now understand contribute to adaptive evolution.

QUESTION:

Why is the connection between inheritance and variation crucial to Darwin's mechanism of natural selection?

2.2

What Is Evolution?

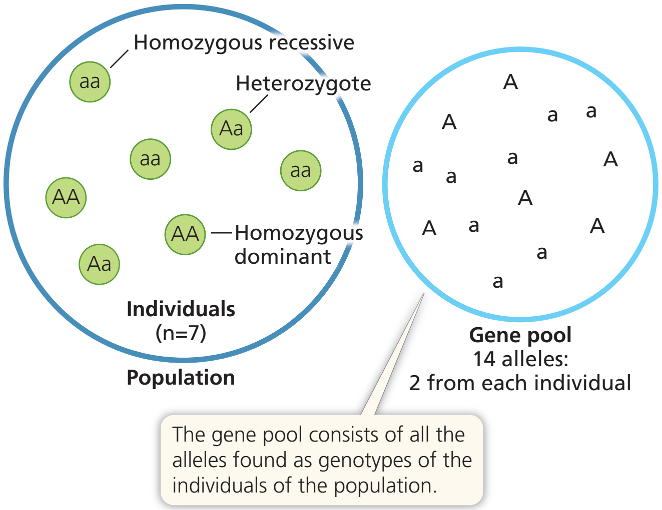
Our description of evolution has thus far been based on the concept as understood in Darwin's time—changes in species over time and the emergence of new species. This concept, while correct, is somewhat vague and certainly nonquantitative. Moreover, it does not incorporate our modern understanding of genetics. Today we define **evolution** as a genetic change in a population over time. What exactly is meant by *genetic change over time*? To answer this question, we must understand how genes and alleles are organized in a population.

How Are Genes Organized in Populations?

The **phenotype** is the characteristic morphology, physiology, and behavior of the organism. The phenotype is the product of the organism's **genotype**, the sum total of its **genes** (as well as interaction of the genotype with the environment—see Section 2.3). A gene is a sequence of DNA that codes for the amino acid sequence that constitutes a specific protein. Some of these proteins are structural elements of the organism. Others are enzymes that produce other structural elements or that catalyze the biochemical reactions that constitute the organism's physiology. The variation among individuals so important to Darwin's theory arises by **mutation**, a random change in the DNA sequence of a gene. Mutations change the amino acid structure of the protein product of the gene and hence its structure and function. Most mutations are deleterious but a few result in a more successful phenotype. It is these new, beneficial variants that provide the basis for natural selection.

Mendelian inheritance and the molecular biology of the gene focus on the characteristics of the individual. However, evolution by natural selection affects a *population* of individuals. The study of these changes is the province of **population genetics**. In population genetics, the focus is on the entire population and its **gene pool**, the sum total of all alleles in the population

- **evolution** The natural process by which species gradually change over time, controlled by changes to the genetic code and whether or not those changes enable an organism to survive in a given environment.
- **phenotype** The characteristics, including morphology, physiology, and behavior, of an individual.
- **genotype** The genetic makeup of the individual that, in concert with the environment, determines the phenotype.
- **gene** A sequence of DNA that encodes the amino acid sequence of a specific protein.
- **mutation** A random change in the DNA sequence of a gene.
- **population genetics** A field of genetics that analyzes the dynamics of genes in an entire population.
- **gene pool** The sum total of all alleles in a population.



The gene pool consists of all the alleles found as genotypes of the individuals of the population.

Figure 2.4 The gene pool. The gene pool consists of all the alleles in all the individuals in a population. In this population of seven individuals, the genotypes are distributed as shown in the right side of the figure. The gene pool consists of all the alleles of those seven individuals. **Analyze: What is the difference between a genotype and the allele frequency?**

(Figure 2.4). We characterize the gene pool for any given trait by the **allele frequencies**, the proportion each allele represents in the population. For example, in Figure 2.4 there are seven individuals with the genotypes shown in the figure. This means that there are 14 alleles for this trait in the population (2 alleles per individual × 7 individuals), as shown in the right side of Figure 2.4. In this gene pool, 6/14 alleles are *A* (0.43), whereas 8/14 (0.57) are *a*. We traditionally assign the variable p to the frequency of the dominant allele, *A* in this case. The frequency of the recessive allele (*a*) is denoted by q. If there are just two alleles at a locus, $p + q = 1.0$.

How Do We Model Changes in the Gene Pool?

Population genetics allows us to formalize the concept of evolution: evolution is a change in allele frequencies, the values of p and q, over time. We mathematically model evolutionary change using a system known as the Hardy-Weinberg equilibrium. Consider a population of 100 individuals with genotype frequencies:

AA	Aa	aa		
36	48	16	=	100

allele frequency The proportion each allele represents in the gene pool.

To calculate p, the frequency of the *A* allele, we need to compute the total number of *A* alleles in the population divided by the total number of alleles. Each homozygous dominant carries two *A* alleles; each heterozygote contains one. If there are 100 individuals in the population, there are 200 total alleles at this locus. Thus, the value of p is calculated as

$$[(36 \times 2) + (48)]/200 = 120/200 = 0.6$$

We calculate the value of q in a similar fashion:

$$[(16 \times 2) + 48]/200 = 80/200 = 0.4$$

If there are only two alleles, $p + q = 1.0$. Thus, we can also calculate q

$$\begin{aligned} 0.6 + q &= 1.0 \\ q &= 0.4 \end{aligned}$$

Now imagine that the individuals in this population mate at random and exactly replace themselves in the next generation. We can calculate the expected distribution of genotypes that results. Homozygous dominant individuals result from two *A* alleles coming together. An easy way to think of the probabilities is to imagine a bag of alleles (the gene pool) made up of 60% *A* alleles and 40% *a* alleles. The probability of reaching into the bag and extracting two *A* alleles is

$$0.6 \times 0.6 = 0.36.$$

This calculation is based on the product rule of probability: the probability of two independent events occurring simultaneously is the product of their independent probabilities. Thus, the probability of two *A* alleles coming together is

$$p \times p = p^2 = (0.6)^2 = 0.36$$

Similarly, for the homozygous recessives, the probability is

$$q \times q = q^2 = (0.4)^2 = 0.16$$

The heterozygote calculation is based on similar reasoning. Imagine that you reach into the gene pool and pull out an allele at random for the gene contributed by the mother, the maternal contribution. The probability that it is *A* is 0.6. Now the probability that the second allele (the paternal contribution) is *a* is 0.4. So it is possible to generate a heterozygote in this way with probability

$$0.6 \times 0.4 = 0.24$$

or

$$p \times q$$

However, there is a second way to generate a heterozygote. The first allele (maternal) could be *a* (with probability 0.4). If so, the probability that the paternal allele is *A* (giving a heterozygote) is 0.6. This order occurs with the probability

$$0.4 \times 0.6 = 0.24$$

or

$$q \times p$$

So, overall the probability of forming a heterozygote is

$$(0.6 \times 0.4) + (0.4 \times 0.6) = 0.24 + 0.24 = 0.48$$

or

$$(p \times q) + (q \times p) = 2pq$$

Thus, the expected genotype frequencies for the population are

AA	Aa	aa
p^2	$2pq$	q^2

And because there are only these three possible genotypes

$$p^2 \qquad 2pq \qquad q^2 = 1.0$$

So, in a population of 100 individuals, the genotype frequencies are

Genotypes	AA	Aa	aa	
Proportion	0.36	0.48	0.16	= 1.0
Number	36	48	16	= 100.0

A population with genotype frequencies that satisfy the equation $p^2 + 2pq + q^2 = 1$ is said to be in **Hardy-Weinberg equilibrium**. The importance of this concept is that in the random mating example we just conducted, there was no change in the genotype or allele frequencies from one generation to the next. If evolution is defined as a change in allele frequencies, the Hardy-Weinberg equilibrium represents the case in which no evolution has occurred. In other words, a population in Hardy-Weinberg equilibrium is not evolving. This leads to the obvious question: What mechanisms change the Hardy-Weinberg equilibrium such that allele frequencies do change?

- **Hardy-Weinberg equilibrium** A mathematical representation of the genotype frequencies of a population in which the allele and genotype frequencies are not changing.

KEY CONCEPTS 2.1

- Evolution proceeds by changes in the genetic composition of a population.
- The gene pool consists of the sum total of all the alleles in the population. Allele frequencies are key components of the gene pool.

THINKING ABOUT ECOLOGY:

Consider a population with the following genotype frequencies:

Genotype	AA	Aa	aa
Number	14	45	40 = 100

a. Is this population in Hardy-Weinberg equilibrium?
b. What are the values of *p* and *q*?
c. If this population mates at random and no other factors affect it, what will be the genotype frequencies in the next generation?
d. Will the values of *p* and *q* change?

- **genetic drift** Random changes in allele frequencies.

- **gene flow** The net movement of alleles to or from a population.

- The Hardy-Weinberg equilibrium describes the genotype frequencies of a population whose allele frequencies are not changing.

QUESTION:

What is the relationship between the allele frequencies (*p* and *q*) and the genotype frequencies in the Hardy-Weinberg equilibrium?

2.3 What Are the Mechanisms of Evolution?

- **mutation pressure** Changes in allele frequency due to the origin of new alleles in the population.

Recall that evolution is defined as a change in allele frequency in a population. In the previous section, we showed that a population that is in H-W equilibrium will remain so. Thus, a population in H-W equilibrium is not evolving. However, H-W equilibrium only occurs if certain conditions hold. Under other circumstances, the equilibrium breaks down and allele frequencies change. By definition, such a population is evolving. What are these crucial conditions?

In the example of a population in H-W equilibrium earlier, we made a set of implicit assumptions.

First, we assumed that none of the genotypes has an advantage in terms of survival or reproduction compared to the others. If, for example, only half of the homozygous recessives survived to reproduce, their frequency would no longer be described by the value q^2. Second, we assumed that the population behaves like a much larger, in fact infinite, population. This assumption is based on the operation of the laws of probability. In very small populations, chance events may result in deviations from the expectations of probability theory. Third, we assumed that there was no net immigration or emigration of particular genotypes. For example, if all the homozygous dominant individuals emigrate, the genotype and allele frequencies will change. Finally, we assumed that there are no new mutations producing novel alleles or changing the dominant allele to recessive or vice versa.

If these four key conditions hold, a population in Hardy-Weinberg equilibrium will remain there with no change in allele frequencies and hence no evolution. Now we see the importance of the Hardy-Weinberg model: its assumptions provide us with potential mechanisms of evolutionary change. If any of these conditions do not hold, evolution occurs (Table 2.1).

Violation of the first assumption leads to evolution by natural selection: differential survival or reproduction of different genotypes. Imagine that a large proportion of the homozygous recessives die before reproducing. The allele frequencies will shift to a higher proportion of the dominant allele (Figure 2.5). The second assumption requires a large population size so that the laws of probability operate as expected. If this assumption does not hold, random changes in allele frequency occur. Random changes in allele frequencies are known as **genetic drift** (Figure 2.6). Violation of the third assumption leads to the net gain or loss of certain alleles by movement of individuals. We refer to this as **gene flow** (Figure 2.7). Finally, new mutations change allele frequencies. The evolutionary change resulting from new mutants is known as **mutation pressure**. Because mutations are so rare, they have a very small impact on overall allele frequencies and we can largely

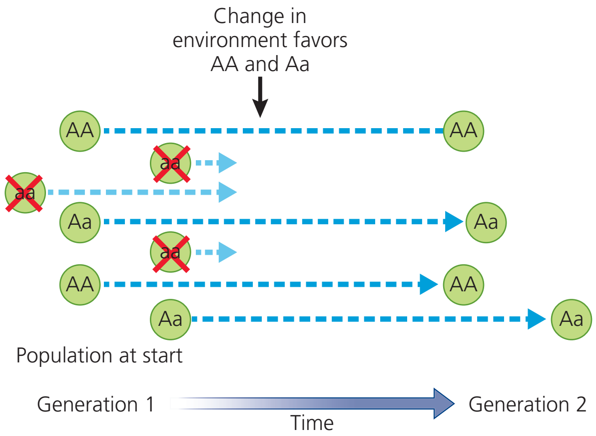


Figure 2.5 Natural selection and heredity. Natural selection occurs over more than one generation. If the homozygous recessives in this population are at a selective disadvantage, their frequency will decrease from one generation to the next. When this occurs, the frequency of the recessive allele (*q*) decreases and the frequency of the dominant allele (*p*) increases. **Analyze: Is it possible for the dominant allele to decrease by natural selection?**

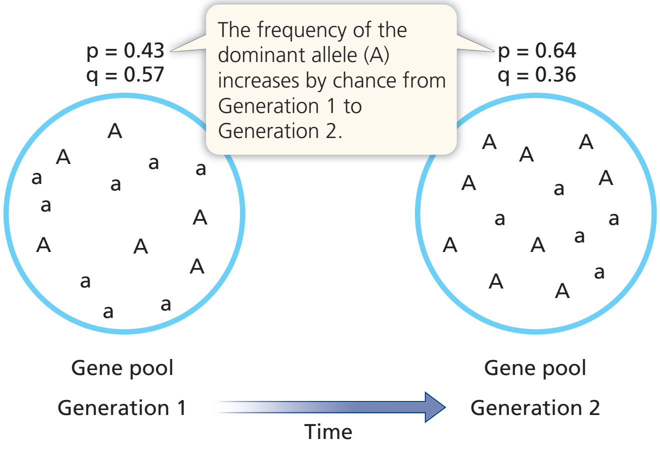


Figure 2.6 Effect of genetic drift on allele frequencies. We expect alleles to be distributed in gametes and in the next generation in the same frequency as generation 1. But in small populations, chance events result in some alleles being under- or overrepresented. Allele frequencies have changed only by chance. **Analyze: Does the value of *p* always increase by drift?**

TABLE 2.1 The assumptions of the Hardy-Weinberg equilibrium and the mechanism of evolution that results if they are violated

ASSUMPTION	MECHANISM IF ASSUMPTION IS VIOLATED
No differential success of genotypes	Natural selection
Population is infinitely large (random mating)	Genetic drift
No net immigration or emigration by genotype	Gene flow
No new mutations	Mutation pressure

ignore their impact; the effects of selection, drift, and gene flow are generally much larger. Of course, mutations are important in that they generate novel alleles on which the other three mechanisms act.

An important point arises from this analysis: there are in fact *four* distinct mechanisms of evolution. Darwin is known for his explication of natural selection. Here is an example of the way in which Darwin was correct but incomplete. Of course, he knew nothing about genes, alleles, or the models developed by Hardy and Weinberg. Let us examine each of these mechanisms in more detail.

How Does Selection Change Allele Frequencies?

Our current understanding of natural selection is based on the Darwinian logic discussed earlier. Selection occurs when a particular genotype does not survive or reproduce in the same proportion as others. We quantify this effect with the **selection coefficient**, *s*: the proportion of a particular genotype that is not represented in the next generation. A selection coefficient of 1.0 means that the allele is lethal. Figure 2.8 shows the impact of different values of *s* on the change in allele frequency during selection.

This process has now been described in detail for a number of organisms and ecological situations. One of the most thoroughly documented examples is the pattern of selection on the bills of Darwin's finches on the Galápagos (Grant and Grant, 1993, 2009). On the island of Daphne, the medium ground finch (*Geospiza fortis*) eats seeds of many sizes but prefers smaller seeds that are easier to crack open. When a major drought occurred in the Galápagos, seed production was severely reduced. As a result, the small seeds preferred by the majority of finches were rapidly depleted. The remaining seeds, mostly the large, hard seeds of *Tribulus cistoides*, are difficult to crack open. Nearly 85% of the finches on Daphne died because their bills were not large and strong enough to crack open these seeds. There was strong selection for deeper, more massive bills, and the proportion of individuals with such bills increased rapidly (Figure 2.9).

Consider this process in terms of the variation in bill sizes before and after the selection event. Bill size is a quantitative trait; that is, bills differ among finches in measurable characteristics (depth, mass, etc.). In many natural populations, variable quantitative traits are distributed in a bell curve (Figure 2.10). When the environment abruptly changed, those individuals with bill sizes at the right edge of the bell curve were favored. Individuals with smaller bills made up most of the 85% that died. As a result, the entire distribution shifted to the right to larger average bill sizes. This form of selection, in which one tail of the bell curve is favored, is known as **directional selection**.

As shown in Figure 2.10, selection can also favor other portions of the bell curve. **Stabilizing selection** occurs

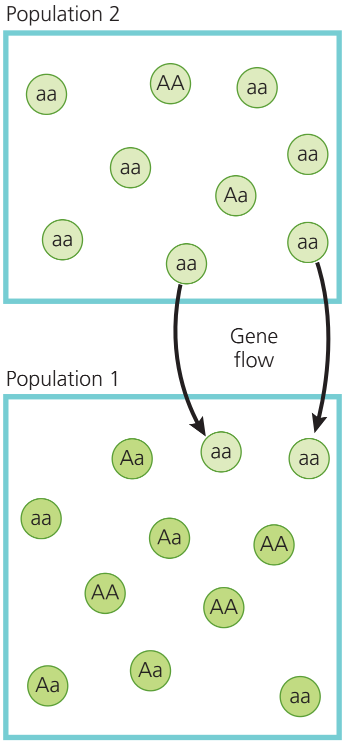


Figure 2.7 Gene flow. Gene flow occurs when there is net immigration (or emigration) of certain genotypes. The movement of alleles changes the allele frequency in the population from which individuals emigrate and the population to which they move. **Analyze: What is the significance of "net" movement?**

selection coefficient (*s*) The proportion of a genotype that is not represented in the next generation due to death or reproductive failure.

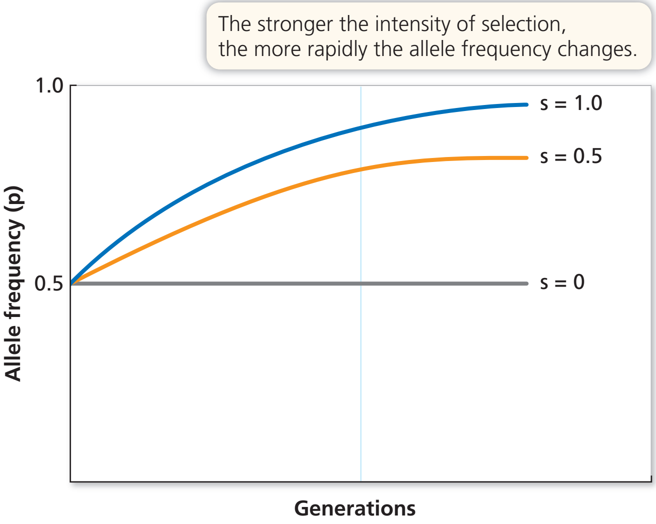


Figure 2.8 Allele frequency. The rate of change in allele frequency by natural selection is determined by the value of *s*, the selection coefficient. If $s = 1.0$, the allele is lethal and all homozygous recessives die. If $s = 0$, there is no selective advantage or disadvantage to the allele. **Analyze: How would these curves change if the dominant allele were lethal?**

THINKING ABOUT ECOLOGY:

Figure 2.8 shows the change in allele frequency under different selection coefficients. In the case of the lethal recessive ($s = 1.0$), the frequency of the dominant allele (p) approaches but never reaches 1.0. Why doesn't selection cause the frequency of the fixation of the dominant allele to reach 1.0?

directional selection A form of selection in which one tail of the phenotypic bell curve is favored.

stabilizing selection A form of selection in which the central portion of the phenotypic bell curve is favored.

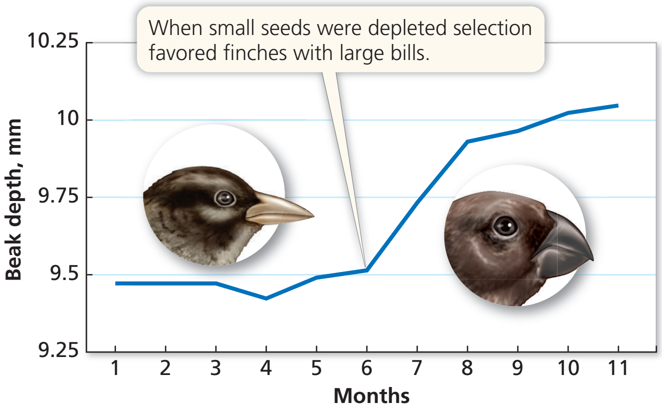


Figure 2.9 The rapid shift in beak depth of finches on Daphne Island following a drought. When the supply of small seeds was depleted, only birds with bills large enough to crack open the large seeds survived (Boag and Grant, 1988). **Analyze: Why is beak depth an important feature of the finch bill and its ability to open seeds?**

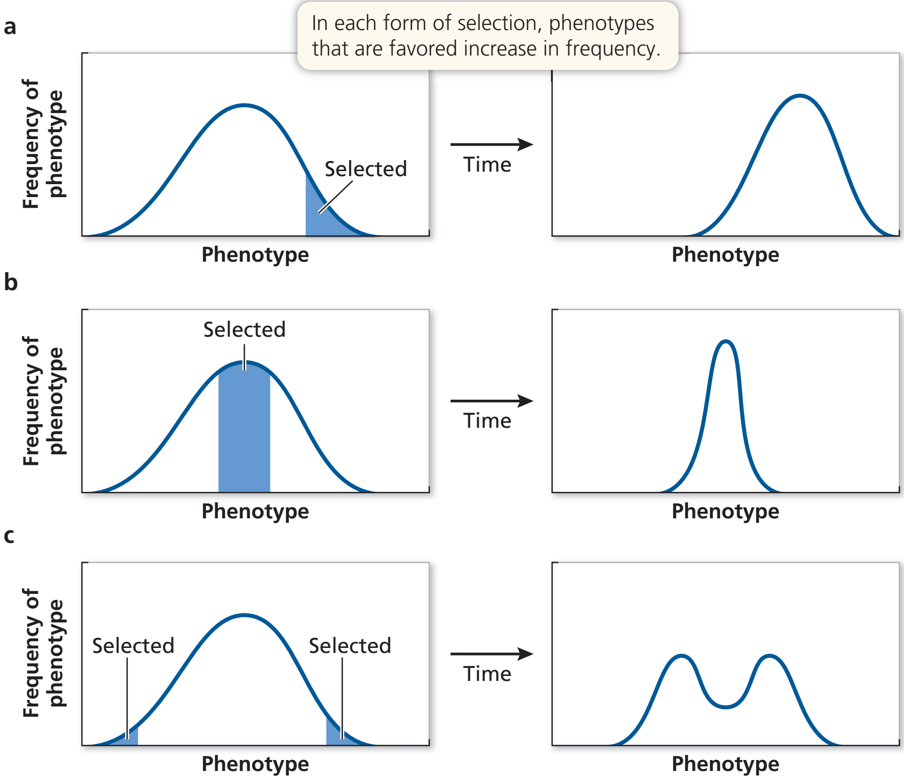


Figure 2.10 Three forms of natural selection. In directional selection (a) one portion of the bell curve is favored. Over time the entire distribution shifts in that direction. Stabilizing selection (b) occurs when the intermediate phenotypes are more fit than the extremes. In disruptive selection (c) the extreme phenotypes are favored compared to the intermediate phenotypes. **Analyze: Is it important whether these phenotypes are genetically determined?**

when individuals in both tails of the curve are at a selective disadvantage and selection favors individuals with intermediate characteristics. The net result is a narrower distribution. In many species, body size is subject to stabilizing selection. There are benefits and costs of extremely large and extremely small body size. Thus it is unlikely that directional selection will continue to push a species to larger and larger *or* to smaller and smaller sizes. Intermediate sizes will contribute proportionally more to the next generation than extreme sizes. There are advantages to large size and to small size, but each also has a cost. This type of selection also illustrates the

THE HUMAN IMPACT

The Evolution of Resistance in Pathogens and Pests

Given the size of the human population and the magnitude of our impact on the natural world, it is no surprise that humans constitute an important selective force on other species. In essence, we have changed the environment for many species, both natural and domesticated. As a result, human activity has provided us with some of the most well-documented examples of natural selection.

Some of the most important cases of anthropogenic evolution occur when we try to control organisms that are harmful to us or to the plants and animals we raise. Antibiotics directed against human pathogens and pesticides designed to control crop pests demonstrate our impact on the evolutionary process. Bacteria gradually develop resistance to each new antibiotic we develop. Because they reproduce so rapidly and occur in such large numbers, the probability that a mutation conferring resistance to an antibiotic is significant. Moreover, many bacterial strains and even different species can transfer genes horizontally, that is, to other unrelated individuals rather than simply to their descendants. The result is the rapid spread of mutations that confer resistance and the origin of strains resistant to multiple antibiotics. MRSA, or methicillin-resistant *Staphlococcus aureus*, is an example of an organism that has acquired resistance to a variety of antibiotics, including the penicillin group (which includes methicillin, dicloxacillin, and nafcillin) as well as the cephalosporin group.

Weed and insect pest resistance to pesticides used on crops is among the most well-studied examples of human-induced evolution. New pesticides are embraced by farmers because their immediate impact on pests and weeds is so great. However, the longer these compounds are in the environment, the more likely their targets are to develop resistance. Notice the rise of insecticide-resistant species in recent decades (Figure 1). Cotton is attacked by many insects and consequently cotton farmers are among the highest users of pesticides. Approximately 40% of all the insecticides used in the United States are applied to cotton. As insects acquire resistance, larger doses of these compounds are required. For example, in just five years the required dose of Endrin required to control the cotton bollworm increased from 0.01 mg/gram of insect larva to 0.13 mg/gram of insect larva. In the same period the required dose of the combination of Toxaphene and DDT increased by a factor of 10.

Resistance to antibiotics or pesticides can be conferred by a variety of mechanisms. Consequently, mutations in a number of biochemical, physiological, and morphological traits may confer resistance. For example, DDT resistance in insects can occur by:

- An increase in lipid content, which allows DDT to be sequestered in fat tissue
- Enzymes that metabolize DDT yielding less toxic products
- Changes in the nervous system that reduce DDT toxicity
- Reduction of the permeability of the cuticle to DDT
- Behaviors that reduce contact with DDT

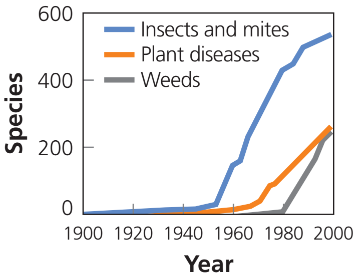


Figure 1 Insecticide and selection. The application of insecticides selects for resistant phenotypes. These resistant forms have increased rapidly after the initial exposure (Weber, 1994).

The specific genes responsible for these phenotypes are scattered among all of the chromosomes in *Drosophila*. None of these traits completely protects the insect from DDT. But each incrementally increases its resistance. One reason for the increase in resistance over time is the accumulation of many different resistance genes in individuals. These superresistant individuals have very high fitness and thus high reproductive success.

The development of herbicide-resistant crops has also accelerated the evolution of pest resistance. Strains of corn and soybeans resistant to the herbicide glyphosate are widely used by American farmers. Some 90% of the soybeans and 70% of the corn planted in the United States are resistant to glyphosate. These resistant crop strains are favored because large amounts of glyphosate can be applied to control weeds without harming the crops. However, prolonged exposure to high concentrations of glyphosate accelerates the evolution of resistance by the weeds. At least one weed, pigweed (*Ameranthus palmeri*), is now fully resistant to glyphosate. Pigweed can grow up to 80 mm per day, attains a height of more than 2 meters, and can damage harvest equipment.

The relevant principles of evolution are clear: natural selection acting on rapidly reproducing pests and pathogens inevitably results in the evolution of resistance to virtually any chemical treatment we develop. At present, our strategy has been the development of new compounds. However, this must be coupled with the judicious use of antibiotics and pesticides that reduces the exposure that accelerates the evolution of resistance.

QUESTION:

How would you describe the evolution of resistance in terms of the selection coefficient, *s*?

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concept of **evolutionary trade-offs**; that is, a feature that confers an advantage in one respect may have a cost in some other important way.

Disruptive selection occurs when the tails of the distribution are favored over the intermediate phenotypes. The monkey flower, *Mimulus luteus*, produces red nectar guides that lead their pollinators, insects and hummingbirds, to the nectar reward and the stamens and anthers where they effect pollination. Note the variation in the size and shape of these nectar guides (Figure 2.11). Research on pollinator preferences in this species showed that insects prefer large guides that point

evolutionary trade-offs Traits that confer a fitness advantage may also have a fitness cost relative to another environmental factor.

disruptive selection A form of selection in which the two tails of the phenotypic bell curve are favored.

Figure 2.11 The color patterns in *Mimulus* flowers guide their pollinators to the nectar. There is variation in the morphology of these guides. Insects prefer large nectar guides; hummingbirds prefer smaller, heart-shaped guides. The result is disruptive selection on the morphology of the guides (Carezza et al., 2003).

directly toward the center of the flower. In contrast, hummingbirds prefer smaller, heart-shaped nectar guides. Because both types of pollinators exert selective pressure on the flowers, their summed impact represents disruptive selection: flowers with intermediate characteristics were the least successful—they were not visited by either birds or insects. The result is that monkey flowers tend to have either large guides or heart-shaped guides (Medel et al., 2003).

How Does Genetic Drift Change Allele Frequencies?

non-Darwinian evolution Genetic drift.

effective population size (N_e) The subset of the total population that mates at random.

Genetic drift is the random change in allele frequency. If, for example, we expect homozygous dominants to occur with the frequency p^2, it is entirely possible that the actual frequency will be lower or higher than this value simply by chance. The phenomenon is more pronounced in small populations. Consider the analogy of flipping a coin. We expect 50% heads and 50% tails. But if you flip a coin only four times, it's entirely possible to get three heads and a tail or even four heads and no tails just by chance. It is far less likely to obtain all heads if you flip the coin 100 times. In a population in which allele frequencies change by drift, evolution is occurring but not by means of natural selection. Thus, genetic drift is also known as **non-Darwinian evolution**.

A number of factors contribute to chance deviation from expectations. However, all are the result of some factor that causes the population to depart from purely random mating in which the laws of probability play out as expected. We define the **effective population size (N_e)** as the subset of the total population that mates randomly. Any characteristic of the population that reduces random mating reduces the effective population size. As N_e becomes smaller than the actual population size, drift becomes more pronounced. For example, if the sex ratio, the proportion of the population that is male and female, is heavily skewed toward one sex, the population will not behave like a large, randomly mating group. Consider a population of 100 individuals. If 90 are female and only 10 are male, those few males must mate with all the females to produce the next generation. In effect, the population is not 100 randomly mating individuals; all the offspring are the product of just 10 males and because of their small numbers, chance events will skew their genetic contribution, leading to shifts in allele frequency.

If we follow a series of populations in which drift occurs over time, the value of p in each population fluctuates, but eventually some reach a p value of 1.0, whereas others fall to 0 (Figure 2.12). When $p = 1.0$, the recessive allele has been lost. In

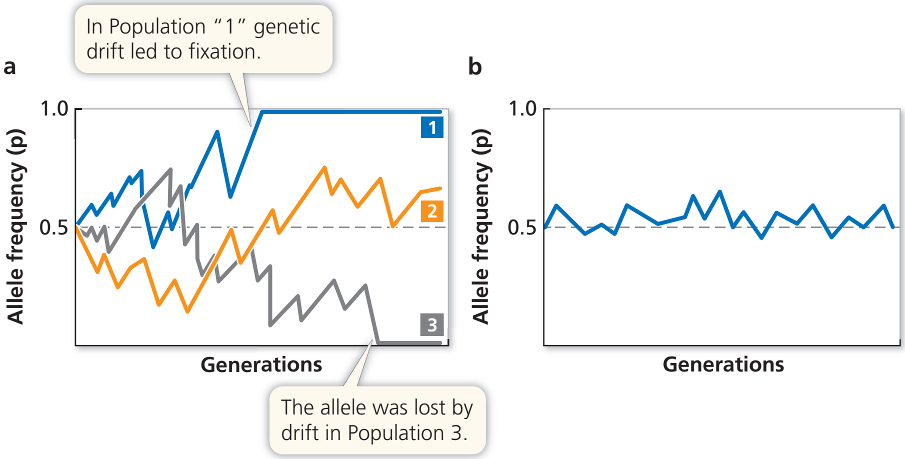
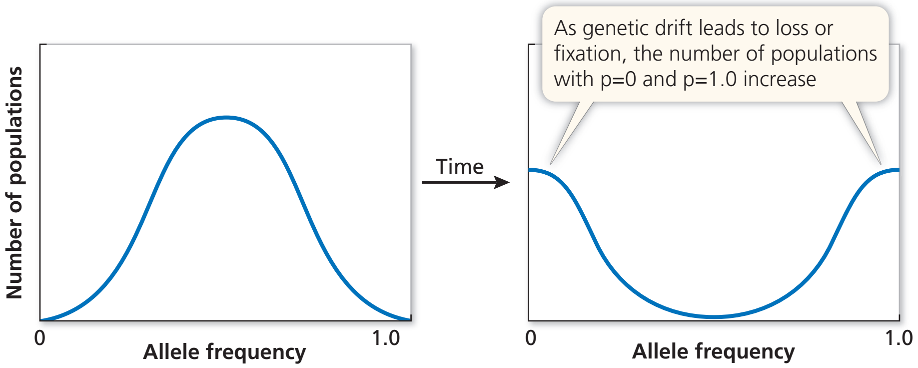


Figure 2.12 Genetic drift. The effects of genetic drift are more pronounced in (a) small populations than in (b) large populations. In (a) each line represents a single, small population. In Population 1, drift led to fixation of the allele. Population 3 lost the allele. In Population 2, the allele persisted until the end of the experiment. **Analyze: Can loss or fixation occur in a large population?**



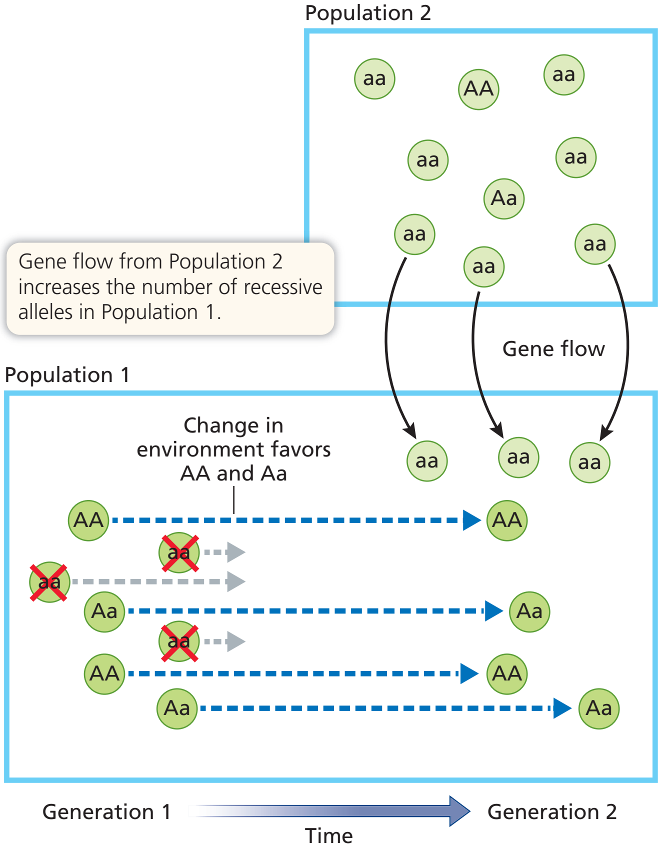
As genetic drift leads to loss or fixation, the number of populations with p=0 and p=1.0 increase

Figure 2.13 Genetic drift leads inevitably to the loss or fixation of alleles. Over time, a group of populations will shift from a normal distribution of allele frequencies to populations in which the allele has either been fixed or lost. **Analyze: Why is the number of populations with fixation eventually the same as the number with loss?**

this case we say that the dominant allele has become fixed. Similarly, when $p = 0$, the dominant allele has been lost and the recessive has been fixed. Loss and fixation of alleles are the inevitable consequence of genetic drift. Because drift is a random process, it is unpredictable whether any particular allele will be lost or fixed. But given enough time, one or the other will occur (Figure 2.13). The effect is evolutionarily important because it means that over time genetic drift, and thus loss and fixation, will reduce the genetic variation in the population. And, of course, it is the variation inherent in the population on which selection operates. A population that has lost variation is susceptible to changes in the environment—it does not have genotypes that might be favored by natural selection in the new environment.

What Are the Effects of Gene Flow?

Gene flow is the net movement of a particular allele to or from the population. If the movement of individuals (and their alleles) in and out of the population is random, there is no effect, that is, no gene flow. But if certain genes disproportionately enter or leave, allele frequencies change. Gene flow may reinforce or oppose the changes that occur by natural selection and drift. If the same genes that are entering the population are those that are increasing randomly within the population by genetic drift, the effect of drift will be more pronounced. Perhaps the most important effect of gene flow occurs when it opposes the changes driven by natural selection. Consider the case in Figure 2.14. Selection favors the dominant allele. However, there is net movement of the *a* allele into the population in the form of homozygous recessives. Clearly, the frequency of *A* will not increase in the way it would under selection alone; gene flow decreases the effect of natural selection. Thus, gene flow has an important impact on evolution by selection: the more isolated the population, the less gene flow and the more effective natural selection can be.



Gene flow from Population 2 increases the number of recessive alleles in Population 1.

Figure 2.14 Gene flow. Gene flow can oppose natural selection if the same alleles that are selected against move into the population from elsewhere. In this example, selection favors the AA and aa genotypes in Population 1. However, gene flow in which aa individuals enter the population maintains their frequency in Population 1 despite their selective disadvantage. **Analyze: Can gene flow accelerate natural selection?**

ON THE FRONTLINE

Gene Flow in Gobies

Gene flow, the net movement of alleles to or from a population, tends to homogenize the gene pool. Moreover, it may counter natural selection by the influx of genes other than those favored by natural selection. The waterfall-climbing Hawaiian goby (*Sicyopterus stimpsoni*) has an amphidromous life history. This means that adult fish inhabit and spawn in fresh water and the larvae drift downstream to the ocean where they mix and mature before returning to the stream as juveniles. Gobies inhabit streams with different topography and characteristics. Some juveniles, such as on the island of Hawai'i, must immediately negotiate steep waterfalls near the mouths of streams. There may be important morphological adaptations to these two environments. The fact that the larvae mature before the juveniles return to streams provides an opportunity for gene flow between the morphs.

Moody et al. (2014) addressed the question of local adaptation in the face of significant gene flow. They analyzed both morphological traits and selectively neutral genetic markers independent of the morphology. This led them to the central hypothesis of the study and its prediction:

HYPOTHESIS 1: Natural selection leads to morphological differences between stream types despite gene flow from a mix of juveniles entering the streams.

PREDICTION 1: Fish should differ morphologically among streams in ways that correspond to the stream morphology and predation risk.

PREDICTION 2: Selectively neutral genetic markers should vary independently among stream populations.

Juvenile gobies were collected near the mouth and below the first waterfall of each stream in order to minimize the time individuals were exposed to the stream environment. Adults were collected from above the first waterfall of each stream. All specimens were digitally photographed and 17 linear morphological traits were measured in each. These traits were subjected to a statistical analysis called discriminant function analysis. This procedure looks for correlations among the 17 traits. It combines correlated traits as a set of new compound morphological variables. The result is a smaller set of morphological variables that are independent of one another. The populations are then graphed with respect to the two variables that most clearly discriminate between the populations. It is possible to identify the specific morphological traits each of these new discriminant variables represents.

The discriminant variables identified differences in adult and juvenile fish from different stream types (Figure 1). Fish from streams with a steep slope and immediate waterfall had large heads and pelvic suckers and a streamlined body axis, which reduces drag during waterfall climbing. In contrast, fish from streams with a shallow slope and slow flow for some distance until the first waterfall had tall, wide bodies, which provide greater thrust for predator avoidance. There was no relationship between morphology and geographic distance among populations; stream type was the significant correlate of morphology.

Neutral genetic markers demonstrated no population differentiation among adult fish. Some juvenile populations showed significant differentiation. However, there was no consistent temporal or spatial pattern to the variation. There was no relationship between juvenile genetic differentiation and geographic distance. It was, however, correlated with morphological differences associated with different stream types.

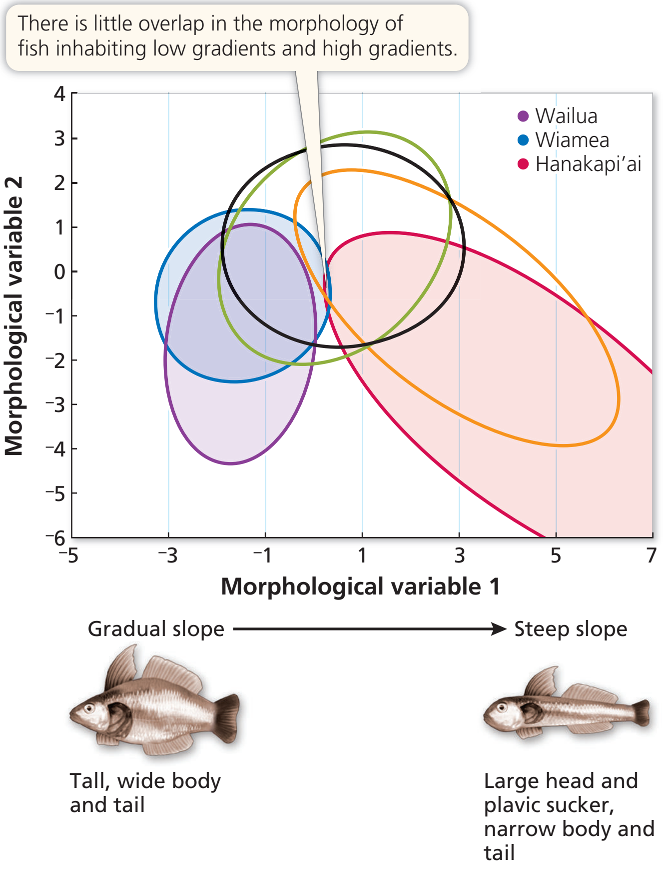

There is little overlap in the morphology of fish inhabiting low gradients and high gradients.

Figure 1 The position of juvenile fish in morphological space, defined by differences in head size, sucker size, body size, and tail size. Each ellipse encloses a different stream population. The ellipses of the lowest slope streams (Wailua and Wiamea) and the steepest slope stream (Hanakapi'ai) are filled in to illustrate the small degree of overlap in morphology among these environmental extremes. **Analyze: What does low overlap in morphological space mean?**

These data support both predictions of the hypothesis. Although larvae from different stream types mix in the ocean, natural selection quickly selects for morphological phenotypes in juveniles appropriate to stream type. The authors conclude that selection is sufficiently intense to overcome the homogenization due to gene flow.

QUESTION:

How do you explain that neutral genetic markers (1) showed no consistent spatial pattern of variation *and* (2) correlated with morphological differences among streams?

KEY CONCEPTS 2.3

- Evolution is defined as change in allele frequencies in a population.
- A population in Hardy-Weinberg equilibrium experiences no change in allele frequency; it is not evolving.
- A population in H-W equilibrium will remain there if (1) there is no differential success of genotypes, (2) the population is large, (3) there is no net movement of alleles in or out of the population, and (4) there are no new mutations.
- The violations of these four respective conditions represent potential mechanisms of evolution: (a) natural selection, (b) genetic drift, (c) gene flow, and (d) mutation pressure.

QUESTION:

What is the difference between the concept of allele frequency and genotype frequency?

2.4 How Do Adaptations Arise?

With this background in evolution, we can return to the origin of adaptations, traits that improve the success of the individual in a particular environment. We can now appreciate Darwin's observations of marine iguanas more fully. Darwin's insight was the intimate relationship between the organism and its environment. His observations of iguanas documented the features that improve their success in their unique environment and way of life.

How Does Selection Lead to Adaptive Change?

The success of a genotype is measured by its fitness. Fitness determines the relative ability of a genotype to obtain genetic representation in the next generation. The frequency of a genotype is reduced by selection against it, that is, by the value of the selection coefficient (*s*). Those genotypes that are less fit decrease in frequency by the amount *s* each generation. Formally, the Hardy-Weinberg analysis includes the selective coefficient and fitness as follows:

Genotype	AA	Aa	aa
Frequency before selection	p^2	$2pq$	q^2
Fitness	1	1	$1 - s$

In this example, there is complete dominance so heterozygotes have the same phenotype and fitness as the homozygous dominants. Note that fitness is a relative term; that is, we measure it in relation to the fitness of other genotypes.

If no other factors are operating, natural selection sorts the genotypes in the population according to their fitness. Because the environment imposes the selective force, the ecology of the organism is central to the adaptive process. The ancestors of modern marine iguanas that had flattened tails and webbed feet were more successful at foraging in the ocean and left more offspring. The result, over many generations, is the set of specialized morphological adaptations we see today.

What Is the Relationship Between Variation and Natural Selection?

Variation among individuals in a population was central to Darwin's logical argument for natural selection. If every individual in the population is identical, there is nothing on which selection can act and adaptive change cannot occur. The population geneticist R.A. Fisher showed mathematically that there is a quantitative relationship between variation and natural selection. According to Fisher's Fundamental Theorem, the increase in fitness of the population is directly proportional to the amount of genetic variation in the population (Fisher, 1930). According to Fisher, most populations are in the process of evolution;

DO THE MATH

Modeling the Rate of Change by Selection

The Hardy-Weinberg equations allow us to model the process of evolution by natural selection. As presented in Section 2.2, the results are qualitative; they show that a particular allele will decline in frequency if selected against. However, we can also use the Hardy-Weinberg model to ask quantitative questions about selection. For example, what determines the rate of change of an allele frequency under selection?

Consider a population in which the homozygous recessives are selected against. Imagine that the selection coefficient represents the proportion that dies each generation. We model this as before, but we algebraically include the effect of natural selection.

	GENOTYPES			POPULATION SIZE
	AA	Aa	aa	
Initial frequency	p^2	$2pq$	q^2	1
Fitness	1	1	$1 - s$	
Proportions after selection	p^2	$2pq$	$q^2 (1 - s)$	$1 - sq^2$
(Determined by multiplying the initial genotype frequency by its fitness)				*Population size is reduced by the loss of homozygous recessives.*

To convert the proportions to genotype frequencies that add up to 1, we divide each by the total population size.

$$p^2/1 - sq^2 + 2pq/1 - sq^2 + q^2(1 - s)/\,1 - sq^2 = 1.$$

Now let us consider what happens to the *A* allele under selection. We expect it to increase, but how fast? To answer this question, we need to calculate the change in *p*, that is, Δp. To do this, we need to find the difference between the initial and new frequency. $\Delta p = p^1 - p$, where p^1 is the new frequency of *A* and *p* is its initial frequency. The value of *p* is based on the total number of *A* alleles divided by the total number of alleles in the population. Remember, each homozygous dominant contains two *A* alleles (that is, $2p^2$) and each heterozygote contains one (that is, $2pq$). The total number of alleles in the population is two times the population size ($2(1 - sq^2)$). So we calculate p^1

$$p^1 = 2p^2 + 2pq/2(1 - sq^2).$$

Because $p + q = 1$, we can algebraically calculate

$$p^1 = 2p^2 + 2pq/2(1 - sq^2) = p(p + q)/1 - sq^2 = p/1 - sq^2.$$

Then to calculate the change in *p*

$$\Delta p = p^1 - p$$

$$\Delta p = p - p(1 - sq^2)/1 - sq^2 = spq^2/1 - sq^2.$$

Now, examine this equation to see what we learn from it. First, because *p* and *q* are less than 1, Δp must be positive. That makes sense: if the recessive is selected against, *p* should increase. It also makes sense that according to this model the rate of change due to selection increases as the selection coefficient increases. But you might not have predicted that Δp also depends on the initial values of *p* and *q*. In other words, the rate of selection varies with the initial allele frequencies. Specifically, when the value of *p* is small (and thus *q* is large), the rate of evolution (Δp) is larger. The rate of increase of a beneficial mutant is higher when it is new, that is, at low frequency. This is one of the values of mathematical models such as this: they can reveal relationships that may not be intuitively obvious to us. And importantly, we have an equation that allows us to predict quantitatively the effect of selection.

they have not come to equilibrium. New favorable mutations arise but have not yet been fixed by natural selection. Consequently, there are fitness differences among individuals on which selection acts.

phenotypic plasticity The ability of an organism to produce different phenotypes in different environments.

The variation Darwin emphasized in his theory must be inherited; that is, it must have a genetic basis. However, there is another important type of variation in populations. **Phenotypic plasticity** is developmental or physiological variation among phenotypes induced directly by the environment. For example, humans born and raised at high elevation differ physiologically from those who live at sea level. They have more red blood cells and hemoglobin, larger lung capacity, and other physiological changes that allow them to function at altitude. If those same individuals developed at sea level, they would not exhibit these changes.

heritability A measure of the proportion of the phenotypic variation for a trait that is determined by additive effects of its genes.

The variation among individuals in a population thus has two possible bases: genetic differences among individuals and phenotypic plasticity in response to differences in the environment. The **heritability** of a trait is the proportion of the phenotypic variation that is due to genetic differences among individuals. Formally, it is the proportion of the phenotypic variation in a population that results from the additive effects of genes. The higher the heritability, the tighter

THE EVOLUTION CONNECTION

Phenotypic Plasticity

Both natural selection and phenotypic plasticity are processes that shape the phenotype. However, they differ in important ways. Natural selection modifies the phenotype by shifting the frequencies of alleles. It operates through the success or failure of individuals. We measure its effect at the population level—as a change in allele frequencies. Also, selection operates over a longer time scale than phenotypic plasticity. Whereas selection requires more than one generation, phenotypic plasticity occurs during the development of the individual.

Phenotypic plasticity is most common in species in which individuals experience more than one environment. For example, the morphology of the olive (*Olea europaea*) varies with the wind environment to which the tree is exposed. Individuals that develop high in the canopy where they are exposed to stronger winds develop smaller leaves and thicker twigs than individuals protected from wind (Garcia-Verdugo et al., 2009). The Trinidad guppy (*Poecilia reticulata*) inhabits some streams that contain predatory fish and others that do not. The probability that they will live long enough to reproduce is lower in streams with predators. The presence of predators triggers a developmental change in guppies: in streams where predators occur, guppies become sexually mature at smaller sizes (Dowdall et al., 2012). In both these cases phenotypic plasticity allows the *individual* to respond appropriately to its environment.

Despite the fundamental differences between natural selection and phenotypic plasticity, both are related to adaptive evolution in important ways. First, phenotypic plasticity is itself an adaptation that arises by natural selection. For example, many plants respond to shading by competing plants with longer stems that increase the exposure of their leaves to light. The light-dependent physiological mechanisms that elongate the internodes, and thus stem length, are the result of natural selection (van Leunen and Fischer, 2005). The environment directly determines the phenotype—but in a way that adapts the plant to its environment.

Second, phenotypic plasticity can either facilitate or retard adaptive evolution by natural selection. For example, phenotypic plasticity can shield the organism from natural selection. If the plastic response produces a moderately successful phenotype, natural selection will have less impact on the gene pool and new adaptations may arise more slowly (de Jong, 2005; Crispo, 2008). Alternatively, plasticity may facilitate colonization of novel and challenging environments. By producing phenotypes tolerant of the new conditions, the organism may persist long enough for natural selection to shape additional adaptations. Salt marsh populations of sticklebacks (*Gasterosteus aculeatus*) putatively exemplify this process. In the estuaries where they live, populations of sticklebacks experience radically different levels of salinity depending on whether they occur near shore where freshwater enters or near the open ocean where salinity is higher. In the estuary of the St. Lawrence River, the freshwater population evolved relatively recently from an ancestral salt-tolerant population. The ancestral population retains considerable phenotypic plasticity for salt tolerance. In contrast, the freshwater population is genetically adapted to the freshwater environment. Apparently the ancestral plastic species was able to colonize and persist in fresh water where a genetically distinct freshwater ecotype eventually arose (McCairns and Bernatchez, 2009).

QUESTION:

Explain how phenotypic plasticity affects the selection coefficient (*s*) and thus the effect of natural selection.

the genetic control of development. The rate of evolution depends on the combination of the intensity of selection and the heritability of the trait. Specifically, the evolutionary response to selection, *R*, is calculated as

$$R = h^2 s.$$

R is typically measured as the proportional change in a character over time.

Selection and variation are causally related in other important ways. Selection leads to geographic variation within species. If a species has a geographic range that encompasses an array of different environments, local selection can lead to significant variation among those locales and environments. Genetically distinct populations that are locally adapted to a particular environment are known as **ecotypes**. The beach mouse, *Peromyscus polionotus*, inhabits a range of environments from coastal Florida to inlands sites in Alabama. Soil color varies across this range from the white beach sands in Florida to dark, loamy soil in Alabama. Coat color in *Peromyscus* varies accordingly. Each local population represents an ecotype—a genetically distinct population whose coat color is locally adaptive (Mullen and Hoekstra, 2008).

ecotype A genetically distinct population that is adapted to local environmental conditions.

Two aspects of the environment determine the probability that local ecotypes will evolve. First, the spatial shift in selection pressure must be relatively abrupt. If selection changes gradually across a large geographic area, it is less likely that a discrete ecotype will arise—the variation in selection pressure is too small. In addition, when the selection pressure is strong, its local effect is more pronounced and there is a greater probability that it will result in a local evolutionary response. Plants, whose individuals are rooted in the ground, exemplify these conditions. Abrupt changes in soil type can lead to ecotypic differentiation over very short distances. For example, mine tailings, the waste piles of rock from which ore has been extracted, often contain high concentrations of heavy metals such as lead or arsenic. Not only do heavy metals constitute a strong selective challenge to the plant, there is often a sharp boundary between the tailings and adjacent nontoxic soil. Local ecotypes have also been demonstrated in populations inhabiting serpentine soil. Serpentine soil is a difficult environment for plants due to its poor water-holding capacity and low concentrations of nitrogen, phosphorus, and potassium. It is also high in magnesium and some heavy metals. Serpentine soil occurs as outcrops surrounded by other soil types. In the sunflower, *Helianthus exilis*, serpentine ecotypes grow within just a few meters of populations on more normal soil. Sambatti and Rice (2006) used molecular techniques to document the sharp genetic differences between serpentine ecotypes and adjacent populations.

THINKING ABOUT ECOLOGY:

A population of sunflowers inhabits a small outcrop of serpentine soil, surrounded by a much larger population on fertile soil. A mutation arises that greatly improves survival on serpentine soil. Selection strongly favors this allele. How would the increase in the frequency of this new allele change if (a) the sunflowers are wind-pollinated or (b) pollinated by bees that move only from one flower to the next adjacent plant?

How Do We Explain Imperfection?

One of the most fascinating things about the study of biology in general and ecology in particular is the remarkable adaptations we observe in nature. The match between organism and environment is so elegant and complex, its study is compelling. Certainly this was Darwin's interest because so much of his career was devoted to understanding adaptive evolution. He was even able to make predictions about adaptations not yet known to science. The Madagascar star orchid (*Angraecum sesquipedale*) is perhaps the most famous example. Darwin observed that the nectar in this flower is located at the bases of extremely long tubes (Figure 2.15). He predicted that an insect pollinator with an extraordinarily long proboscis exists on the island. Nearly 100 years later a hawk moth with precisely the requisite proboscis, *Xanthopan morganii praedicta,* was finally discovered there.

Although we tend to focus on these examples of the remarkable fit between organisms and their environment, it is important to recognize that not all organisms are perfectly adapted. Imperfection is common in the natural world—there

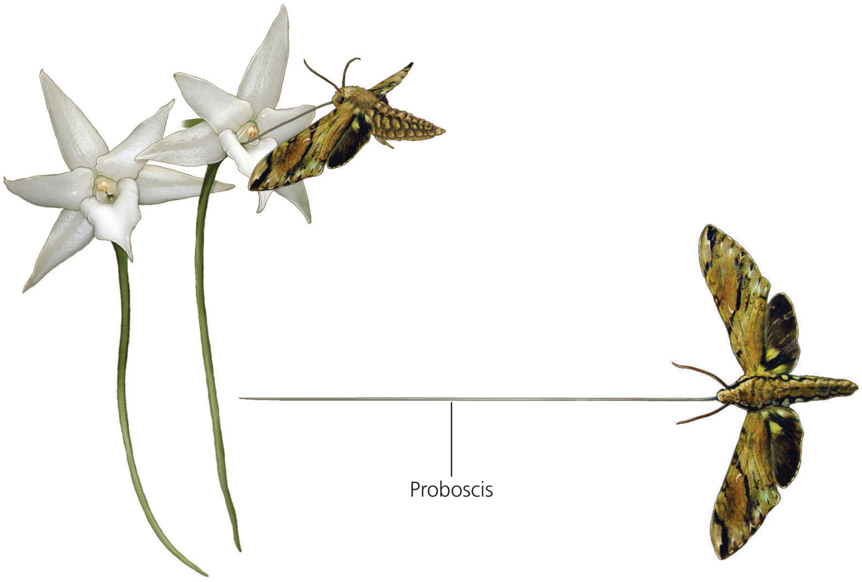


Figure 2.15 Mutually beneficial adaptations. In the Madagascar star orchid the nectar is found at the base of a very long tube. Darwin predicted the existence of a hawk moth with a proboscis long enough to reach the nectar of the star orchid. It wasn't until 100 years after Darwin's description that the hawk moth was discovered.