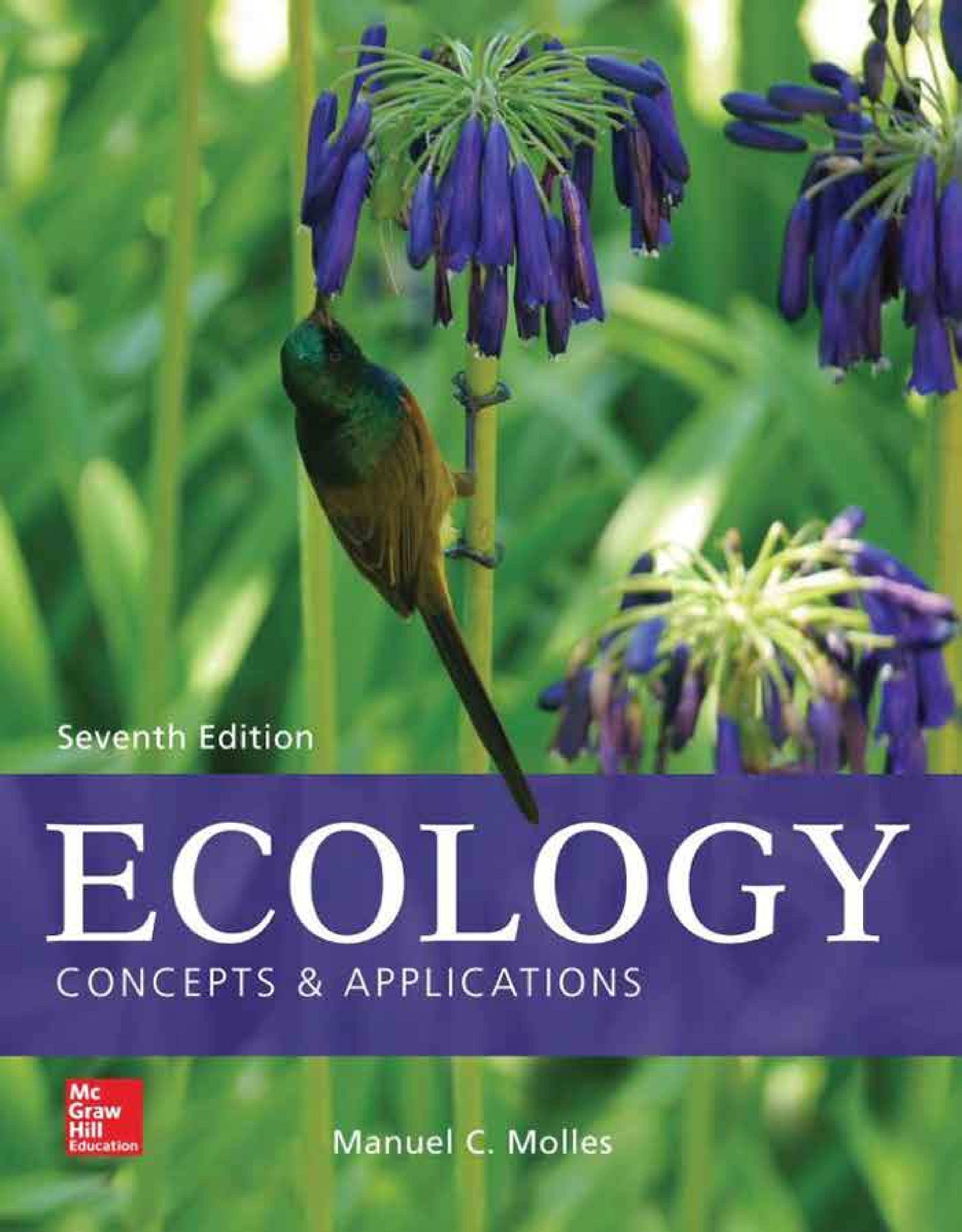

Seventh Edition

ECOLOGY

CONCEPTS & APPLICATIONS

Mc Graw Hill Education

Manuel C. Molles

SEVENTH EDITION

Ecology

Concepts and Applications

Manuel C. Molles Jr.
University of New Mexico

Mc Graw Hill Education

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About the Author

Manuel C. Molles Jr. is an emeritus Professor of Biology at the University of New Mexico, where he has been a member of the faculty and curator in the Museum of Southwestern Biology since 1975 and where he continues to write and conduct ecological research. He received his B.S. from Humboldt State University and his Ph.D. from the Department of Ecology and Evolutionary Biology at the University of Arizona. Seeking to broaden his geographic perspective, he has taught and conducted ecological research in Latin America, the Caribbean, and Europe. He was awarded a Fulbright Research Fellowship to conduct research on river ecology in Portugal and has held visiting professor appointments in the Department of Zoology at the University of Coimbra, Portugal, in the Laboratory of Hydrology at the Polytechnic University of Madrid, Spain, and at the University of Montana's Flathead Lake Biological Station.

Originally trained as a marine ecologist and fisheries biologist, the author has worked mainly on river and riparian ecology at the University of New Mexico. His research has covered a wide range of ecological levels, including behavioral ecology, population biology, community ecology, ecosystem ecology, biogeography of stream insects, and the influence of a large-scale climate system (El Niño) on the dynamics of southwestern river and riparian ecosystems. His current research concerns the influence of climate change and climatic variability on the dynamics of populations and communities along steep gradients of temperature and moisture in the mountains of the Southwest. Throughout his career, Dr. Molles has attempted to combine research, teaching, and service, involving undergraduate as well as graduate students in his ongoing projects. At the University of New Mexico, he has taught a broad range of lower division, upper division, and graduate courses, including Principles of Biology, Evolution and Ecology, Stream Ecology, Limnology and Oceanography, Marine Biology, and Community and Ecosystem Ecology. He has taught courses in Global Change and River Ecology at the University of Coimbra, Portugal, and General Ecology and Groundwater and Riparian Ecology at the Flathead Lake Biological Station. Dr. Manuel Molles was named Teacher of the Year by the University of New Mexico for 1995–1996 and Potter Chair in Plant Ecology in 2000. In 2014, he received the Eugene P. Odum Award from the Ecological Society of America based on his "ability to relate basic ecological principles to human affairs through teaching, outreach and mentoring activities."

Dedication

To Mary Anne
and
Keena

Brief Contents

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Section III
POPULATION ECOLOGY

Preface

This book was written for students taking their first undergraduate course in ecology. I have assumed that students in this one-semester course have some knowledge of basic chemistry and mathematics and have had a course in general biology, which included introductions to physiology, biological diversity, and evolution.

Organization of the Book

An evolutionary perspective forms the foundation of the entire textbook, as it is needed to support understanding of major concepts. The textbook begins with a brief introduction to the nature and history of the discipline of ecology, followed by section I, which includes two chapters on natural history—life on land and life in water and a chapter on population genetics and natural selection. Sections II through VI build a hierarchical perspective through the traditional subdisciplines of ecology: section II concerns adaptations to the environment; section III focuses on population ecology; section IV presents the ecology of interactions; section V summarizes community and ecosystem ecology; and finally, section VI discusses large-scale ecology and includes chapters on landscape, geographic, and global ecology. These topics were first introduced in section I within a natural history context. In summary, the book begins with the natural history of the planet, considers portions of the whole in the middle chapters, and ends with another perspective of the entire planet in the concluding chapter. The features of this textbook were carefully planned to enhance the students' comprehension of the broad discipline of ecology.

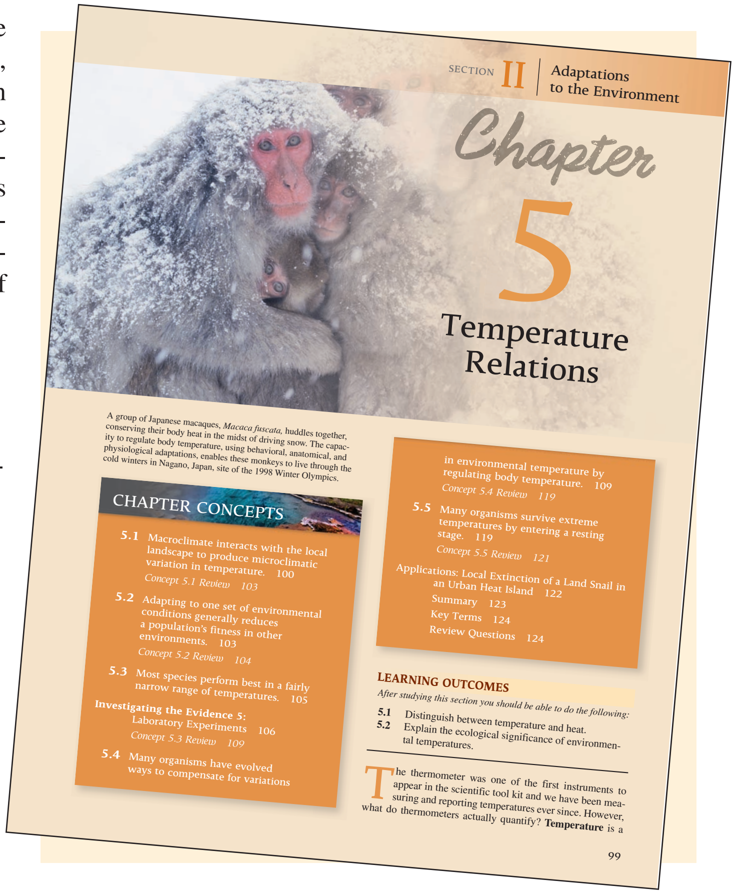
Features Designed with the Student in Mind

All chapters are based on a distinctive learning system, featuring the following key components:

Student Learning Outcomes: Educators are being asked increasingly to develop concrete student learning outcomes for courses across the curriculum. In response to this need and to help focus student progress through the content, all sections of each chapter in the seventh edition begin with a list of detailed student learning outcomes.

Introduction: The introduction to each chapter presents the student with the flavor of the subject and important background information. Some introductions include historical events related to the subject; others present an example of an ecological process. All attempt to engage students and draw them into the discussion that follows.

Concepts: The goal of this book is to build a foundation of ecological knowledge around key concepts. I have found that while beginning ecology students can absorb a few central concepts well, they can easily get lost in a sea of details. The key concepts are listed at the beginning of each chapter to alert the student to the major topics to follow and to provide a place where the student can find a list of the important points covered in each chapter. The sections in which concepts are discussed focus on published studies and, wherever possible, the scientists who did the research are introduced. This case-study approach supports the concepts with evidence, and introduces students to the methods and people that have created the discipline of ecology. Each concept discussion ends with a series of concept review questions to help students test their knowledge and to reinforce key points made in the discussion.



SECTION II Adaptations to the Environment

Chapter 5

Temperature Relations

A group of Japanese macaques, *Macaca fuscata,* huddles together, conserving their body heat in the midst of driving snow. The capacity to regulate body temperature, using behavioral, anatomical, and physiological adaptations, enables these monkeys to live through the cold winters in Nagano, Japan, site of the 1998 Winter Olympics.

CHAPTER CONCEPTS

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LEARNING OUTCOMES

After studying this section you should be able to do the following:

5.1 Distinguish between temperature and heat.
5.2 Explain the ecological significance of environmental temperatures.

The thermometer was one of the first instruments to appear in the scientific tool kit and we have been measuring and reporting temperatures ever since. However, what do thermometers actually quantify? **Temperature** is a

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Illustrations: A great deal of effort has been put into the development of illustrations, both photographs and line art. The goal has been to create more effective pedagogical tools through skillful design and use of color, and to rearrange the traditional presentation of information in figures and captions. Much explanatory material is located within the illustrations, providing students with key information where they need it most. The approach also provides an ongoing tutorial on graph interpretation, a skill with which many introductory students need practice.

Detailed Explanations of Mathematics: The mathematical aspects of ecology commonly challenge many students taking their first ecology course. This text carefully explains all mathematical expressions that arise to help students overcome these challenges. In some cases, mathematical expressions are dissected in illustrations designed to complement their presentation in the associated narrative.

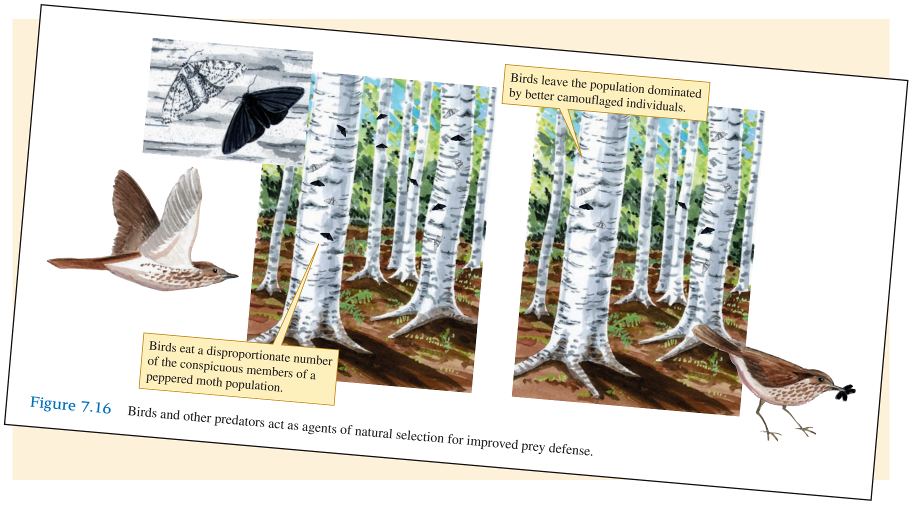

Figure 7.16 Birds and other predators act as agents of natural selection for improved prey defense.

Visualizing a process involving a predator and its prey.

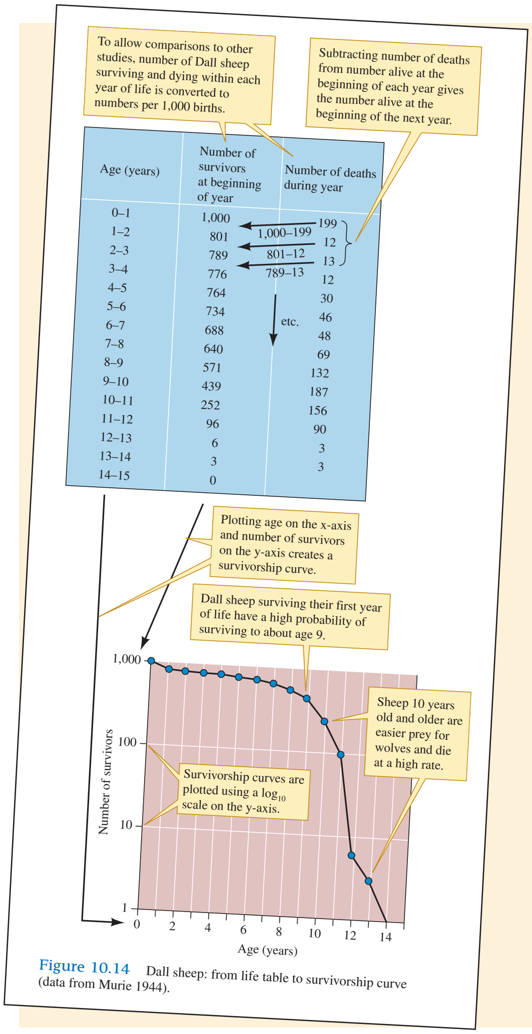

Figure 10.14 Dall sheep: from life table to survivorship curve (data from Murie 1944).

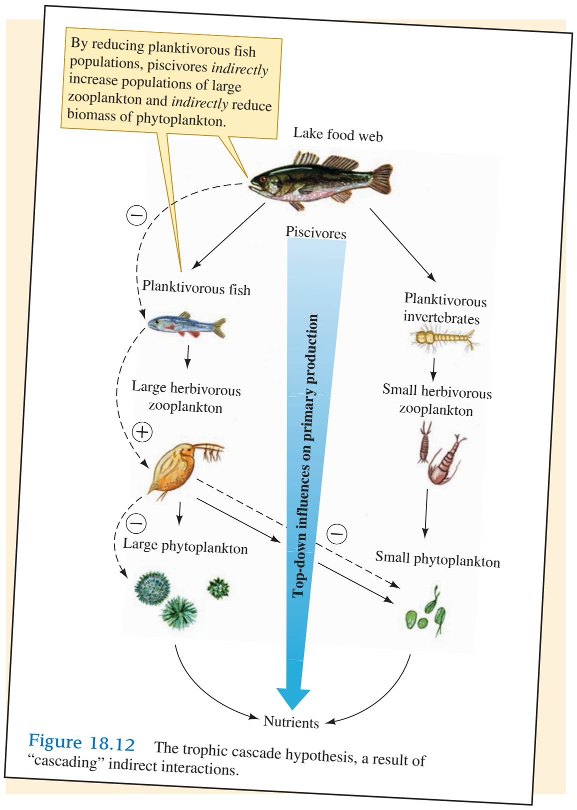

Figure 18.12 The trophic cascade hypothesis, a result of "cascading" indirect interactions.

Helps students work with and interpret quantitative information, involving converting numerical information into a graph.

Provides a visual representation of a hypothesis involving a set of complex ecological interactions.

"Investigating the Evidence" Boxes: These readings offer "mini-lessons" on the scientific method, emphasizing statistics and study design. They are intended to present a broad outline of the process of science, while also providing step-by-step explanations. The series of boxes begins in chapter 1 with an overview of the scientific method, which establishes a conceptual context for more specific material in the next 21 chapters. The last reading wraps up the series with a discussion of electronic literature searches. Each Evidence box ends with one or more questions, under the heading "Critiquing the Evidence." This feature is intended to stimulate critical thinking about the box content.

Applications: Many undergraduate students want to know how abstract ideas and general relationships can be applied to the ecological problems we face in the contemporary world. They are concerned with the practical side of ecology and want to know more about how the tools of science can be applied. Including a discussion of applications in each chapter motivates students to learn more of the underlying principles of ecology. In addition, it seems that environmental problems are now so numerous and so pressing that they have erased a once easy distinction between general and applied ecology.

End-of-Chapter Material:

- ***Summary*** The chapter summary reviews the main points of the content. The concepts around which each chapter is organized are boldfaced and redefined in the summary to reemphasize the main points of the chapter.
- ***Key Terms*** The listing of key terms provides page numbers for easy reference in each chapter.
- ***Review Questions*** The review questions are designed to help students think more deeply about each concept and to reflect on alternative views. They also provide a place to fill in any remaining gaps in the information presented and take students beyond the foundation established in the main body of the chapter.

End-of-Book Material:

- ***Appendixes*** One appendix, "Statistical Tables," is available to the student for reference. Answers to Concept Review questions and answers to Critiquing the Evidence are now available with the book's instructor resources.
- ***Glossary*** List of all key terms and their definitions.
- ***References*** References are an important part of any scientific work. However, many undergraduates are distracted by a large number of references within the text. One of the goals of a general ecology course should be to introduce these students to the primary literature without burying them in citations. The number of citations has been reduced to those necessary to support detailed discussions of particular research projects.
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Laboratory Experiments

LEARNING OUTCOMES

After studying this section you should be able to do the following:

5.12 Describe the basic design of a laboratory experiment.
5.13 Discuss the relative strengths and weaknesses of laboratory experiments and field observations in ecological studies.

One of the most powerful ways to test a hypothesis is through an experiment. Experiments used by ecologists generally fall into one of two categories—field experiments and laboratory experiments. Field and laboratory experiments generally provide complementary information or evidence, and differ somewhat in their design. Here we discuss the design of laboratory experiments.

In a laboratory experiment, the researcher attempts to keep all factors relatively constant except one. The one factor that is not kept constant is the one of interest to the experimenter and it is the one that the experimenter varies across experimental conditions. Let's draw an example of a laboratory experiment discussed in this chapter (see p. 000). Based upon published studies, Michael Angilletta (2001) concluded that geographically separated populations of the eastern fence lizard, *Sceloporus undulatus,* may differ physiologically or behaviorally.

Angilletta designed a laboratory experiment to test the hypothesis that populations of *S. undulatus* from regions with significantly different climates differ in how temperature affects their rates of metabolizable energy intake. The results of that experiment are summarized by figure 5.10. What we want to consider here is the design of the experiment that produced those results. What factors do you think Angilletta may have attempted to control in this experiment? First, he used similar numbers of lizards from the two populations. He tested 20 lizards from both populations at 33°C, 13 from New Jersey at 30° and 36°C, and 14 from South Carolina at 30° and 36°C. A second factor that Angilletta controlled was lizard size. Lizards from both populations used in the experiments had an average body mass of approximately 5.4 g. Since males and females may differ physiologically, Angilletta included approximately equal numbers of males and females in his experiments. He also was careful to expose all the lizards to the same quality of light and to the same numbers of hours of light and darkness and he maintained them in the same kinds of experimental enclosures. Angilletta also fed all the lizards in his experiment the same type of food: live crickets. The list could go on but these are the major factors controlled in this experiment.

Now, what factors did Angilletta vary in that experiment? For each study population, New Jersey or South Carolina, he varied a single factor: temperature. In the experiment, Angilletta maintained lizards from New Jersey and South Carolina at three temperatures: 30°, 33°, and 36°C and estimated their rates of metabolizable energy intake at these three temperatures. Angilletta's experiment revealed that lizards from both populations have a maximum metabolizable energy intake at 33°C. This result suggests, contrary to the study's hypothesis, that the optimum temperature for feeding does not differ for the two populations. However, the experiment also showed that at 33°C *S. undulatus* from South Carolina have a higher metabolizable energy intake compared to lizards from New Jersey. This result provides evidence of the geographic differences that Angilletta thought might exist across the range of *S. undulatus*. The power of this experiment to reveal the influence of temperature on lizard performance resulted from the ability of the researcher to control all significant factors but the one of interest. In this case the main factor of interest was temperature.

CRITIQUING THE EVIDENCE 5

1. What is the greatest strength of laboratory experiments in ecological research?
2. Why do ecologists generally supplement information resulting from laboratory experiments with field observations or experiments?

the United States, living in a broad diversity of climatic zones (fig. 5.9). Taking advantage of this wide range of environmental conditions, Michael Angilletta (2001) studied the temperature relations of *S. undulatus* over a portion of its range. In one of his studies, Angilletta determined how temperature influences metabolizable energy intake, or MEI. He measured MEI as the amount of energy consumed (C) minus energy lost in feces (F) and uric acid (U), which is the nitrogen waste product produced by lizards. We can summarize MEI in equation form as:

$$MEI = C - F - U$$

Angilletta studied two populations from New Jersey and South Carolina, regions with substantially different climates. He collected a sample of lizards from both populations and maintained portions of his samples from both populations at 30°, 33°, and 36°C. Angilletta kept his study lizards in separate enclosures and provided them with crickets that he had weighed to the nearest 0.1 mg as food. Since he had determined the energy content of an average cricket, Angilletta was able to determine the energy intake by each lizard by counting the number of crickets they ate and calculating the energy content of that number. He determined the energy lost as feces (F) and uric acid (U) by collecting all the feces and uric acid produced by each lizard and then drying and weighing this material. He estimated the average energy content of feces and uric acid using a bomb calorimeter.


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Applications

Local Extinction of a Land Snail in an Urban Heat Island

LEARNING OUTCOMES

After studying this section you should be able to do the following:

5.21 Outline changes in the distribution of the snail *Arianta arbustorum* around Basel, Switzerland, between 1900 and 1990.
5.22 Explain how urbanization generally creates a "heat island."
5.23 Review the evidence that temperature changes around the city of Basel are responsible for local extinctions of the snail *Arianta arbustorum.*

Between 1906 and 1908, a Ph.D. candidate named G. Bollinger (1909) studied land snails in the vicinity of Basel, Switzerland. Eighty-five years later, Bruno and Anette Baur (1993) carefully resurveyed Bollinger's study sites near Basel for the presence of land snails. In the process, they found that at least one snail species, *Arianta arbustorum,* had disappeared from several of the sites. This discovery led the Baurs to explore the mechanisms that may have produced extinction of these local populations.

A. arbustorum is a common land snail in meadows, forests, and other moist, vegetated habitats in northwestern and central Europe. The species lives at altitudes up to 2,700 m in the Alps. The Baurs report that the snail is sexually mature at 2 to 4 years and may live up to 14 years. Adult snails have shell diameters of 16 to 20 mm. The species is hermaphroditic. Though individuals generally mate with other *A. arbustorum,* they can fertilize their own eggs. Adults produce one to three batches of 20 to 80 eggs each year. They deposit their eggs in moss, under plant litter, or in the soil. Eggs generally hatch in 2 to 4 weeks, depending upon temperature. The egg is an especially sensitive stage in the life cycle of land snails. *A. arbustorum* often lives alongside *Cepea nemoralis,* a land snail with a broader geographic distribution that extends from southern Scandinavia to the Iberian peninsula.

How did the Baurs document local extinctions of *A. arbustorum?* If you think about it a bit, you will probably realize that it is usually easier to determine the presence of a species than its absence. If you do not encounter a species during a survey, it may be that you just didn't look hard enough. Fortunately, the Baurs had over 13 years of experience doing fieldwork on *A. arbustorum* and knew its natural history well. For instance, they knew that it is best to search for the snails after rainstorms, when up to 70% of the adult population is active. Consequently, the Baurs searched Bollinger's study sites after heavy rains. They concluded that the snail was absent at a site only after two 2-hour surveys failed to turn up either a living individual or an empty shell of the species.

The Baurs found *A. arbustorum* still living at 13 of the 29 sites surveyed by Bollinger near Basel. Eleven of these remaining populations lived in deciduous forests and the other two lived on grassy riverbanks. However, the Baurs could not find the snail at 16 sites. Eight of these sites had been urbanized, which made the habitat unsuitable for any land snails because natural vegetation had been removed. Between 1900 and 1990 the urbanized area of Basel had increased by 500%. However, the eight other sites where *A. arbustorum* had disappeared were still covered by vegetation that appeared suitable. Four of these sites were covered by deciduous forest, three were on riverbanks, and one was on a railway embankment. These vegetated sites also supported populations of five other land snail species, including *C. nemoralis.*

What caused the extinction of *A. arbustorum* at sites that still supported other snails? The Baurs compared the characteristics of these sites with those of the sites where *A. arbustorum* had persisted. They found no difference between these two groups of sites in regard to slope, percent plant cover, height of vegetation, distance from water, or number of other land snail species present. The first major difference the Baurs uncovered was in altitude. The sites where *A. arbustorum* was extinct had an average altitude of 274 m. The places where it survived had an average altitude of 420 m. The places where the snail had survived were also cooler.

A thermal image of the landscape taken from a satellite showed that surface temperatures in summer around Basel ranged from about 17° to 32.5°C. Surface temperatures where *A. arbustorum* had survived averaged approximately 22°C, while the sites where the species had gone extinct had surface temperatures that averaged approximately 25°C. The sites where the snail was extinct were also much closer to very hot areas with temperatures greater than 29°C. Figure 5.34 is based on the Baurs' thermal image of the area around Basel and shows where the snail was extinct and where it persisted.

The Baurs attributed the higher temperatures at the eight sites where the snail is extinct to heating by thermal radiation from the urbanized areas of the city. Buildings and pavement store more heat than vegetation. In addition, the cooling effect of evaporation from vegetation is lost when an area is built over. Increased heat storage and reduced cooling make urbanized landscapes thermal islands. Heat energy stored in urban centers is transferred to the surrounding landscape through thermal radiation, H_r.

The Baurs documented higher temperatures at the sites near Basel where *A. arbustorum* is extinct and identified a well-studied mechanism that could produce the higher temperatures of these sites. However, are the temperature differences they observed sufficient to exclude *A. arbustorum* from the warmer sites? The researchers compared the temperature relations of *A. arbustorum* and *C. nemoralis* to find some clues. They concentrated their studies on the influence of temperature on reproduction by these two snail species.

The eggs of each species were incubated at four temperatures—19°, 22°, 25°, and 29°C. Notice that these temperatures fall within the range measured by the satellite image (see fig. 5.34). The eggs of both species hatched at a high rate at 19°C. However, at higher temperatures, their eggs hatched at significantly lower rates. At 22°C, less than 50% of *A. arbustorum* eggs hatched, while the eggs of *C. nemoralis* continued to hatch at a high rate. At 25°C, no *A. arbustorum* eggs hatched, while approximately 50% of the *C. nemoralis* eggs hatched. At 29°C,

New to the Seventh Edition

The seventh edition expands the pedagogy by beginning all sections of every chapter with a list of student learning outcomes—over 450 student learning outcomes in all. These outcomes are largely based on fundamental learning outcomes for material covered in the text:

1. Define key terms.
2. Explain the main concepts.
3. Evaluate the strength of research presented in support of main concepts, including a critique of study design.
4. Interpret statistical evidence bearing on concepts, expressed in graphical and numerical form.
5. Apply the main concepts to interpretation of new situations.

A content thread focused on global change has been developed and distributed across chapters, emphasizing global climate change. Students and instructors increasingly look for ways to connect the concepts and practice of ecological science to environmental issues arising from global climate change. The present edition explores how species are adjusting their distributions and their critical life history events as climate changes. The final chapter ends with a review of projected impacts of climate change on ecosystems and human populations, infrastructure, and economic systems.

This edition also builds on previous discussions of human disturbance of ecosystems to consider how damaged ecosystems can be restored. The extent and intensity of human impact on the biosphere grows with our population and expanding global economy. While climate change is the most prominent aspect of contemporary global change, other facets, such as damage or destruction of ecosystems, also call for solutions. As a result, there is greater need to restore damaged communities and ecosystems. In this context, the new edition adds an introduction to the practice of ecological restoration, focusing on how the process of restoring ecosystems can benefit from concepts developed in academic studies of community and ecosystem succession.

The relationship between biodiversity and ecosystem function is introduced through the positive influence of primary producer diversity on rates of primary production. Studies of biodiversity and ecosystem function are key elements in ecology's foundation. Connecting these elements helps create conceptual coherence across the discipline. A growing body of recent research does just that. Therefore, this edition includes a new section on the connection between biodiversity and ecosystem function.

The seventh edition introduces developments in trophic ecology that build on classical models of predator-prey interactions. The early to middle twentieth century was a golden age for theoretical ecology. However, those developments have not stopped. Contemporary ecologists continue to build on that legacy, improving our representation and understanding of ecological systems as they do so. The seventh edition updates the discussion of consumer functional response by introducing alternative models based on the ratio of prey to predator numbers rather than prey density per se. This discussion is coupled with reviews of experimental and field studies that support the ratio-dependent models.

The present edition connects ratio-dependent models of functional response to patterns of consumer abundance and secondary production in ecosystems. Previous editions have provided thorough coverage of the ecology of primary production in terrestrial and aquatic ecosystems, but secondary production has received much less attention. This seventh edition addresses this deficiency by including a section that covers the fundamentals of secondary production. The introduction to secondary production in this edition is presented in the context of consumer responses to variations in primary production.

New supplementary materials are placed online. Materials cut from the sixth edition and those previously cut from the fifth and fourth editions are available online. Suggested readings have been updated and placed online, along with answers to Concept Review and Critiquing the Evidence questions.

Significant Chapter-by-Chapter Changes

In **chapters 1 to 23,** numbered learning outcomes were added to all concept discussions and Evaluating the Evidence and Applications features. The average number of learning outcomes added to each chapter is 20.

In **chapter 10,** a new Applications feature explores evidence that plant and animal ranges have shifted northward and to higher latitudes in the Northern Hemisphere during the recent period of rapid global warming. This is the beginning of the global climate change thread in the seventh edition. However, the presentation builds on earlier content in chapter 1 on population responses to climate change, including evolutionary responses, and in chapter 4 on temperature relations of organisms.

In **chapter 12,** a new Applications feature reviews studies that have shown shifts in the timing of flowering in plants and of migration in birds in response to climate warming. The discussion complements the earlier discussion of shifts in species ranges in chapter 10 by demonstrating that climate warming is not just inducing organisms to move in response to global warming but also adjusting their life histories.

In **chapter 13,** the Lotka-Volterra equations have been modified from previous editions to make them more standard, less cluttered, and easier for students to follow, which is essential, since these equations are the foundation of the mathematical ecology covered in the text.

In **chapter 14,** we revisit predator functional responses first introduced in chapter 7 by evaluating alternatives to those models. The Lotka-Volterra models of predator-prey interactions published in the early twentieth century stimulated a long line of research. More recently, researchers have offered alternatives that help identify where those classical mathematical models, with their simplifying assumptions, apply and where alternative formulations better account for aspects of predator-prey interactions, particularly at larger spatial and longer temporal scales. The discussion in this chapter reviews how recent ratio-dependent functional response models better predict predator functional responses in experimental and natural settings. The discussion helps to dispel the idea that mathematical ecology ceased to develop in the mid-twentieth century and reinforces the complementary roles of theoretical, experimental, and observational studies.

In **chapter 18,** a new concept connects primary producer diversity to higher levels of primary production. The chapter also includes a new concept featuring the relationship between levels of primary production and secondary production. This discussion provides a basis for introducing the fundamentals of secondary production. This addition also revisits the ratio-dependent functional responses introduced in chapter 14 by extending the implications of those models beyond predator functional response to the trophic structure of ecosystems. The treatment also formally introduces secondary production, filling a conceptual gap in previous editions.

In **chapter 20,** the fields of ecological restoration and restoration ecology are introduced for the first time. Human impact on the environment has altered ecological communities and ecosystems in nearly every corner of the planet. Restoring structure and function to these systems emerges as one of the great contemporary ecological challenges. Increasingly ecologists addressing this challenge are turning to the conceptual framework of ecological succession to guide their work. Examples of such work are included in this chapter to help bridge the historical divide between ecological theory and restoration practice.

In **chapter 23,** the discussion of the Antarctic ozone hole has been updated to 2013, including 35 years of data from NASA on the size of the ozone hole. The pattern shows that the maximum size of the Antarctic ozone hole has stabilized, signaling a basis for ozone recovery predicted by atmospheric scientists over the next 50 years, providing a bit of good planetary news. The growing body of climate change research, published since the earlier editions of *Ecology Concepts and Applications,* has greatly improved understanding of how earth's changing climate will impact ecosystems and human populations, if not stabilized. A discussion of these impacts concludes this edition, underscoring the relevance of ecological knowledge to sustaining natural as well as human-centered systems.

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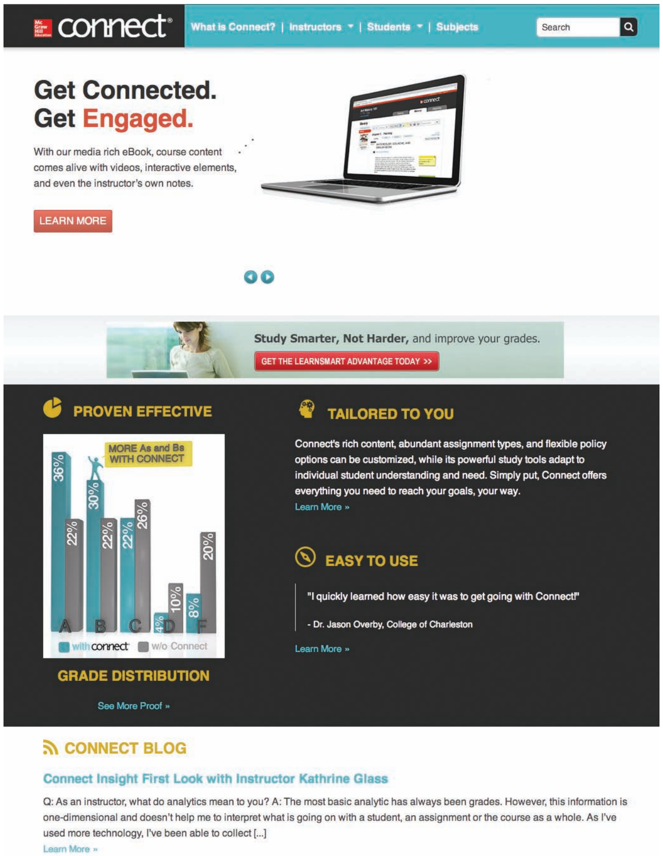

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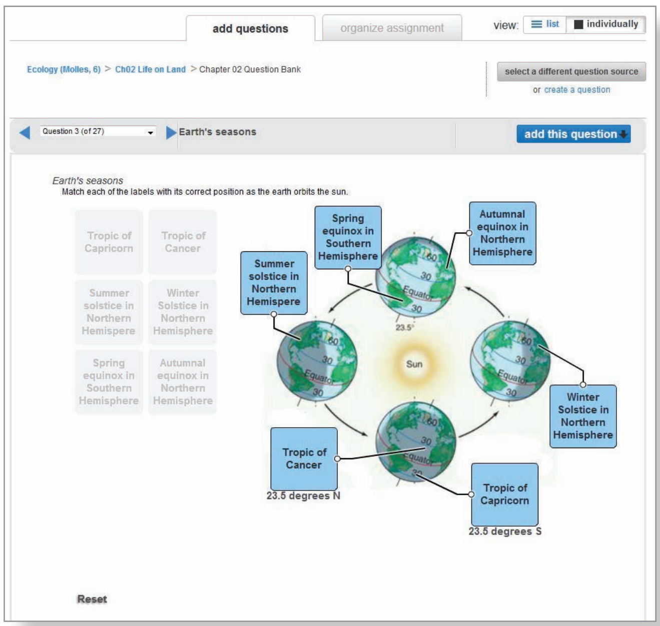

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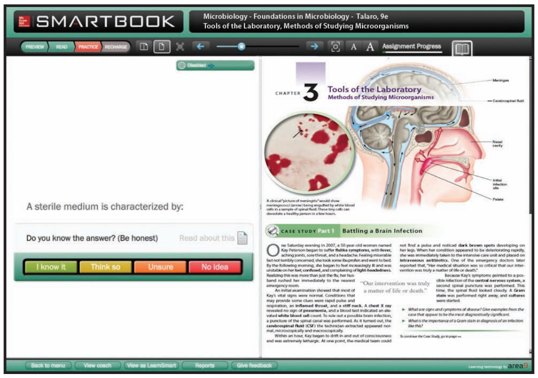

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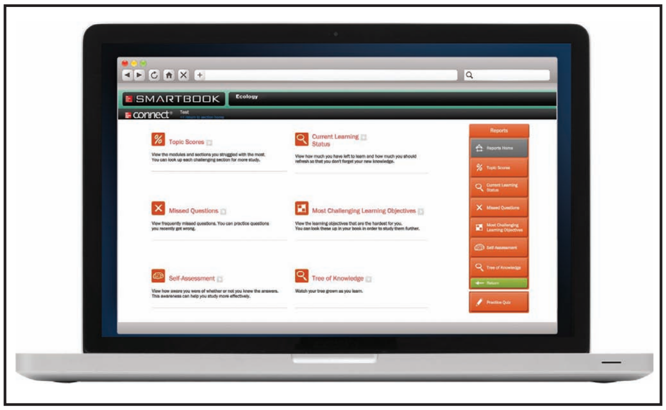

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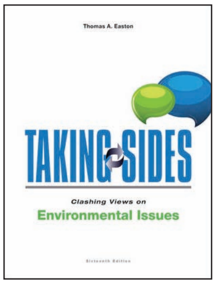

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Chapter 1

Introduction to Ecology

Historical Foundations and Developing Frontiers

A yellow-rumped warbler, *Dendroica coronata,* feeding young. Ecological studies of warblers have made fundamental contributions to the growth of ecological understanding.

CHAPTER CONCEPTS

LEARNING OUTCOME

After studying this section you should be able to do the following:

1.1 Discuss the concept of environment as it pertains to the science of ecology.

What is ecology? **Ecology,** the study of relationships between organisms and the environment, has been a focus for human study for as long as we have existed as a species. Our survival has depended upon how well we could observe variations in the environment and predict the responses of organisms to those variations. The earliest hunters and gatherers had to know the habits of their animal prey and where to find food plants. Later, agriculturists had to be aware of variations in weather and soils and of how such variation might affect crops and livestock.

Today, most of earth's human population live in cities and most of us have little direct contact with nature. More than ever before, though, the future of our species depends on how well we understand the relationships between organisms and the environment. Our species is rapidly changing earth's environment, yet we do not fully understand the consequences of these changes. For instance, human activity has increased the quantity of nitrogen cycling through the biosphere, changed land cover across the globe, and increased the atmospheric concentration of CO_2. Changes such as these threaten the diversity of life on earth and may endanger our life support system. Because of the rapid pace of environmental change at the dawn of the twenty-first century, it is imperative that we continue as ardent students of ecology.

Behind the simple definition of ecology lies a broad scientific discipline. Ecologists may study individual organisms, entire forests or lakes, or even the whole earth. The measurements made by ecologists include counts of individual organisms, rates of reproduction, or rates of processes such as photosynthesis and decomposition. Ecologists often spend as much time studying nonbiological components of the environment, such as temperature or soil chemistry, as they spend studying organisms. Meanwhile, the "environment" of organisms in some ecological studies are other species. While you may think of ecologists as typically studying in the field, some of the most important conceptual advances in ecology have come from ecologists who build theoretical models or do ecological research in the laboratory. Clearly, our simple definition of *ecology* does not communicate the great breadth of the discipline or the diversity of its practitioners. To get a better idea of what ecology is, let's briefly review the scope of the discipline.

1.1 Overview of Ecology

LEARNING OUTCOMES

After studying this section you should be able to do the following:

1.2 Describe the levels of ecological organization, for example, population, studied by ecologists.

1.3 Distinguish between the types of questions addressed by ecologists working at different levels of organization.

1.4 Explain how knowledge of one level of ecological organization can help guide research at another level of organization.

Ecologists study environmental relationships ranging from those of individual organisms to factors influencing global-scale processes. This broad range of subjects can be organized by arranging them as levels in a hierarchy of ecological organization, such as that imbedded in the brief table of contents and the sections of this book. Figure 1.1 attempts to display such a hierarchy graphically.

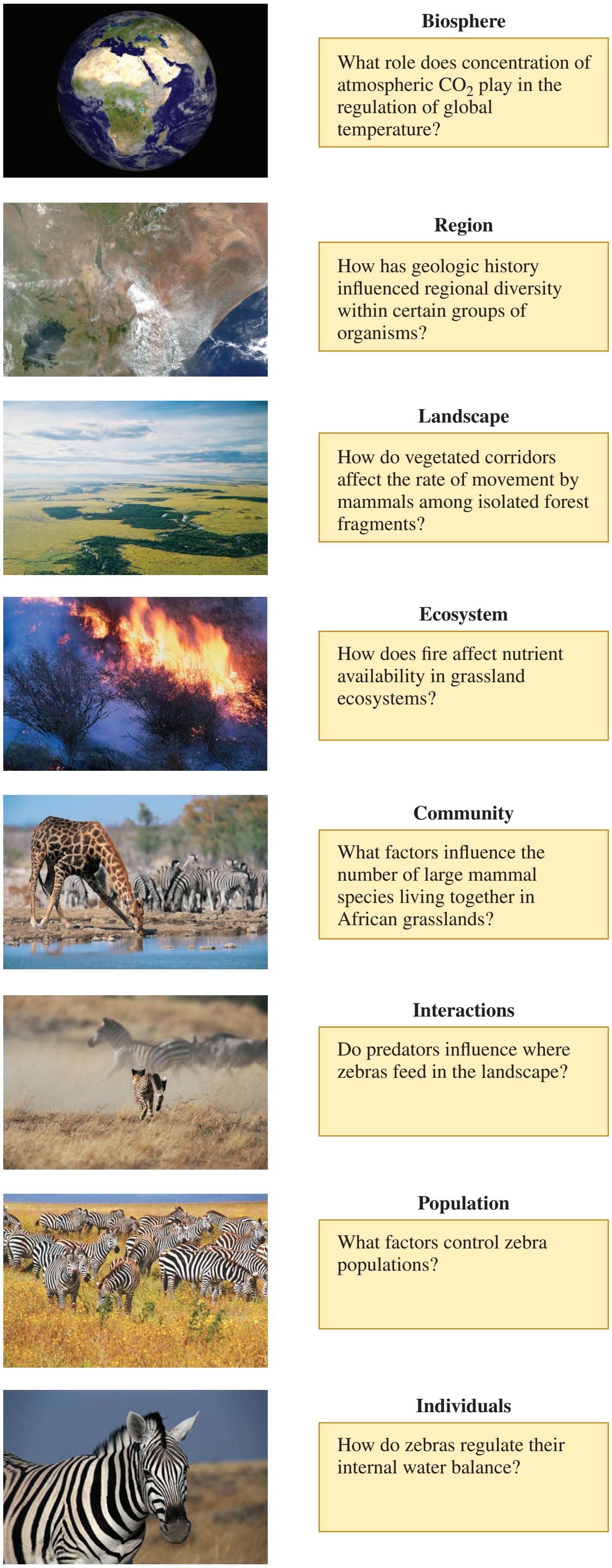


Figure 1.1 Levels of ecological organization and examples of the kinds of questions asked by ecologists working at each level. These ecological levels correspond broadly to the sections of this book.

Historically, the ecology of individuals, which is presented at the base of figure 1.1, has been the domain of physiological ecology and behavioral ecology. Physiological ecologists have emphasized the **evolution** (a process by which populations change over time) of physiological and anatomical mechanisms by which organisms solve problems posed by physical and chemical variation in the environment. Meanwhile, behavioral ecologists have focused principally on evolution of behaviors that allow animals to survive and reproduce in the face of environmental variation. Physiological and behavioral ecology are informed by evolutionary theory, as are all other areas of ecology.

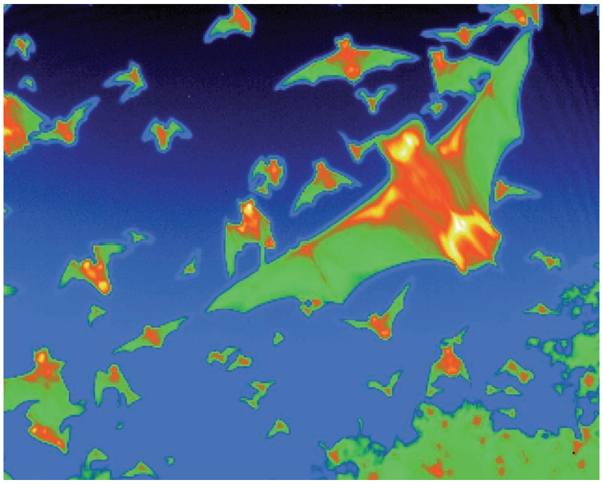
There is a strong conceptual linkage between ecological studies of individuals and of populations particularly where they concern evolutionary processes. Population ecology is centered on the factors influencing population structure and process, where a population is a group of individuals of a single species inhabiting a defined area. The processes studied by population ecologists include adaptation, extinction, the distribution and abundance of species, population growth and regulation, and variation in the reproductive ecology of species. Population ecologists are particularly interested in how these processes are influenced by nonbiological and biological components of the environment.

Bringing biological components of the environment into the picture takes us to the next level of organization, the ecology of interactions such as predation, parasitism, and competition. Ecologists who study interactions between species have often emphasized the evolutionary effects of the interaction on the species involved. Other approaches explore the effect of interactions on population structure or on properties of ecological communities.

The definition of an ecological community as an association of interacting species links community ecology with the ecology of interactions. Community and ecosystem ecology have a great deal in common, since both are concerned with the factors controlling multispecies systems. However, the objects of their study differ. While community ecologists concentrate on the organisms inhabiting an area, ecosystem ecologists include the physical and chemical factors influencing the community and focus on processes such as energy flow and decomposition.

To simplify their studies, ecologists have long attempted to identify and study isolated communities and ecosystems. However, all communities and ecosystems on earth are open systems subject to exchanges of materials, energy, and organisms with other communities and ecosystems. The study of these exchanges, especially among ecosystems, is the intellectual territory of landscape ecology. However, landscapes are not isolated either but part of geographical regions subject to large-scale and long-term regional processes. These regional processes are the subjects of geographic ecology. Geographic ecology in turn leads us to the largest spatial scale and highest level of ecological organization—the **biosphere,** the portions of the earth that support life, including the land, waters, and atmosphere.

While this description of ecology provides a brief preview of the material covered in this book, it is a rough sketch and highly abstract. To move beyond the abstraction represented by figure 1.1, we need to connect it to the work of the scientists who have created the discipline of ecology. To do so, let's briefly review the research of ecologists working at a broad range of ecological levels emphasizing links between historical foundations and some developing frontiers (fig. 1.2).



(a)

(b)

Figure 1.2 Two rapidly developing frontiers in ecology. (*a*) **Aeroecology:** the interdisciplinary study of the ecology of the earth-atmosphere boundary (Kunz et al. 2008). New tools, such as the Indigo/FLIR Merlin mid thermal camera that took this thermal infrared image of flying Brazilian free-tailed bats, *Tadarida braziliensis,* have opened this developing frontier in ecology. This image depicts variation in the surface temperature of these bats. Thermal infrared technology makes it possible not only to detect and record the presence of free-ranging nocturnal organisms, but also to investigate their physiology and ecology in a noninvasive manner (see chapter 5, p. 114). (*b*) **Urban ecology:** the study of urban areas as complex, dynamic ecological systems, influenced by interconnected, biological, physical, and social components. As ecologists focus their research on the environment where most members of our species live, they have made unexpected discoveries about the ecology of urban centers such as the city of Baltimore (see chapter 19, p. 432).

Concept 1.1 Review

1. How does the level of ecological organization an ecologist studies influence the questions he or she poses?
2. While an ecologist may focus on a particular level of ecological organization shown in figure 1.1, might other levels of organization be relevant, for example, does an ecologist studying factors limiting numbers in a population of zebras need to consider the influences of interactions with other species or the influences of food on the survival of individuals?

1.2 Sampling Ecological Research

LEARNING OUTCOMES

After studying this section you should be able to do the following:

1.5 Describe some emerging frontiers in ecology.
1.6 Explain how the use of stable isotopes has extended what it is possible to know about the ecology of warblers.
1.7 Compare the spatial and temporal scales addressed by the research of Robert MacArthur, Nalini Nadkarni, and Margaret Davis.

Ecologists design their studies based on their research questions, the temporal and spatial scale of their studies, and available research tools. Because the discipline is so broad, ecological research can draw from all the physical and biological sciences. The following section of this chapter provides a sample of ecological questions and approaches to research.

The Ecology of Forest Birds: Old Tools and New

Robert MacArthur gazed intently through his binoculars. He was watching a small bird, called a warbler, searching for insects in the top of a spruce tree. To the casual observer it might have seemed that MacArthur was a weekend bird-watcher. Yes, he was intensely interested in the birds he was watching, but he was just as interested in testing ecological theory.

The year was 1955, and MacArthur was studying the ecology of five species of warblers that live together in the spruce forests of northeastern North America. All five warbler species, Cape May (*Dendroica tigrina*), yellow-rumped (*D. coronata*), black-throated green (*D. virens*), blackburnian (*D. fusca*), and bay-breasted (*D. castanea*), are about the same size and shape and all feed on insects. Theory predicted that two species with identical ecological requirements would compete with each other and that, as a consequence, they could not live in the same environment indefinitely. MacArthur wanted to understand how several warbler species with apparently similar ecological requirements could live together in the same forest.

The warblers fed mainly by gleaning insects from the bark and foliage of trees. MacArthur predicted that these warblers might be able to coexist and not compete with each other if they fed on the insects living in different zones within trees. To map where the warblers fed, he subdivided trees into vertical and horizontal zones. He then carefully recorded the amount of time warblers spent feeding in each.

MacArthur's prediction proved to be correct. His quantitative observations demonstrated that the five warbler species in his study area fed in different zones in spruce trees. As figure 1.3 shows, the Cape May warbler fed mainly among new needles and buds at the tops of trees. The feeding zone of the blackburnian warbler overlapped broadly with that of the Cape May warbler but extended farther down the tree. The black-throated green warbler fed toward the trees' interiors. The bay-breasted warbler concentrated its feeding in the interior of trees. Finally, the yellow-rumped warbler fed mostly on the ground and low in the trees. MacArthur's observations showed that though these warblers live in the same forest, they extract food from different parts of that forest. He concluded that feeding in different zones may reduce competition among the warblers of spruce forests.

MacArthur's study (1958) of foraging by warblers is a true classic in the history of ecology. However, like most studies it raised as many questions as it answered. Scientific research is important both for what it teaches us directly about nature and for how it stimulates other studies that improve our understanding. MacArthur's work stimulated numerous studies of competition among many groups of organisms, including warblers. Some of these studies produced results that supported his work and others produced different results. All added to our knowledge of competition between species and of warbler ecology.

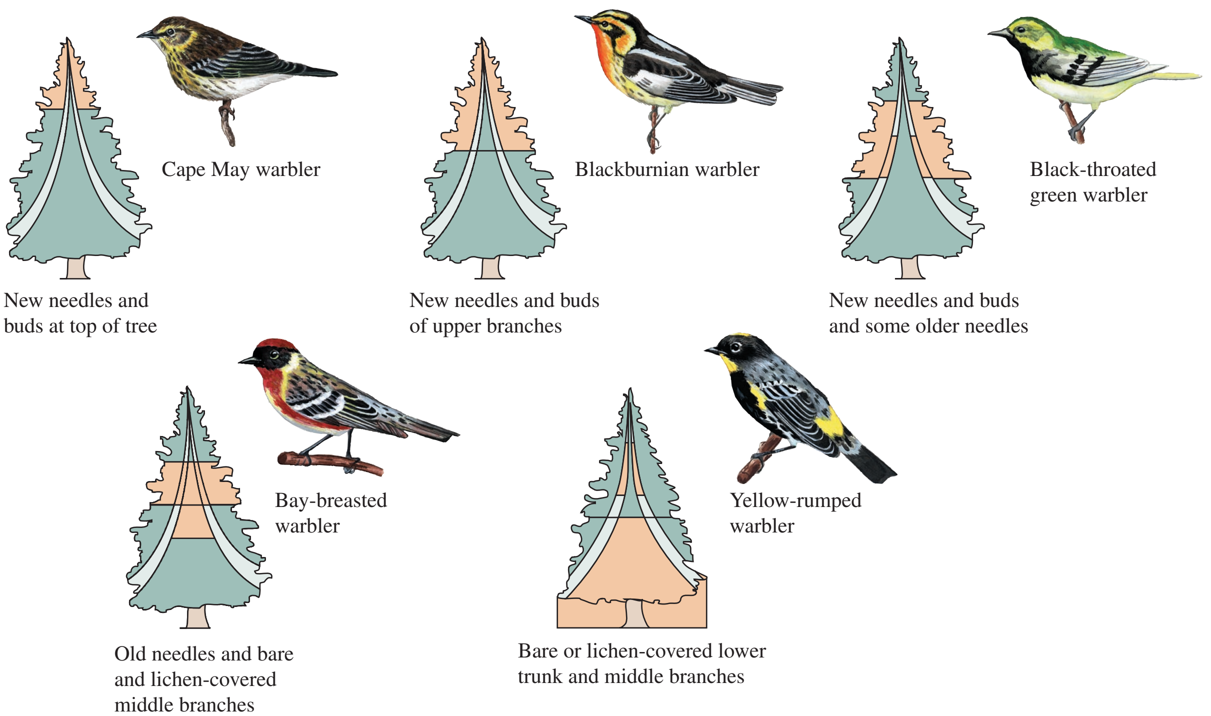


Figure 1.3 Warbler feeding zones shown in beige. The several warbler species that coexist in the forests of northeastern North America feed in distinctive zones within forest trees.

Figure 1.4 A male American redstart, *Setophaga ruticilla.* Mature male American redstarts are highly territorial, dominating high-quality feeding territories in their tropical wintering grounds, pushing most female redstarts and young males into poorer-quality feeding habitats.

Nearly half a century after Robert MacArthur studied the feeding ecology of warblers through the lenses of his binoculars, a team of Canadian and U.S. scientists led by Ryan Norris (Norris et al. 2005) worked to develop tools capable of penetrating the feeding habitats of wide-ranging migratory birds. The object of their study was the American redstart (*Setophaga ruticilla*), another colorful member of the warbler family Parulidae (fig. 1.4). American redstarts, like the warblers studied by MacArthur, are long-distance migrants, nesting in temperate North America but spending their winters mainly in tropical Central America, northern South America, and the Caribbean islands.

Historically, studies of wide-ranging bird species, such as the American redstart, have focused mainly on their temperate breeding grounds. However, observations by ecologists had long suggested that the success of an individual migratory bird during the breeding season may depend critically on the environmental conditions it experienced on its tropical wintering grounds. For example, it has been well established that male migratory birds, arriving early on the breeding grounds, are generally in better physical condition compared to those arriving later. Early arrivals also generally obtain the best breeding territories and have higher reproductive success.

Variation in arrival times and physical condition led ecologists to ponder the connection between events on the wintering grounds and subsequent reproductive success among birds in their breeding habitats. To answer such a question, we need a great deal of information, including where individual birds live on the wintering grounds, how the winter habitat correlates with physical condition during migration, how winter habitat influences time of arrival on the breeding grounds, and whether winter habitat correlates with reproductive success on the breeding grounds. Clearly, the amount of information required to answer such questions, concerning environments separated by thousands of kilometers (fig. 1.5), exceeds what one person, or even a large team, can learn through the lenses of binoculars.

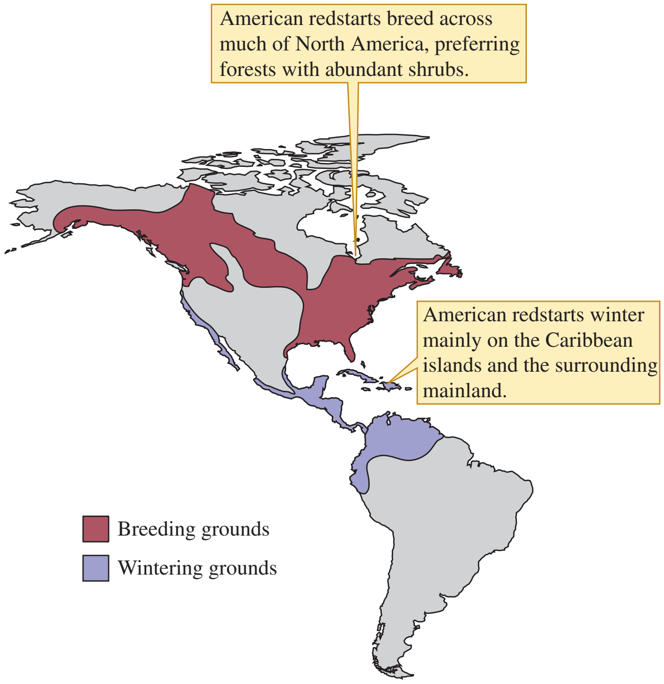


Figure 1.5 Map of the breeding and wintering grounds of the American redstart, *Setophaga ruticilla.*

Often, ecologists have pioneered the use of more powerful research tools, as the complexity of their questions have increased. A tool to which ecologists turn increasingly to understand the ecology of migratory birds is **stable isotope analysis** (see chapter 6, p. 145). Isotopes of a chemical element, for example, isotopes of carbon, have different atomic masses as a result of having different numbers of neutrons. Carbon, for instance, has three isotopes (listed in order of increasing mass): ^{12}C, ^{13}C, and ^{14}C. Of these three, ^{12}C and ^{13}C are stable isotopes because they do not undergo radioactive decay, whereas ^{14}C decays radioactively and is therefore unstable. Stable isotopes have proven useful in the study of ecological processes—for example, identifying food sources, because the proportions of various isotopes differ across the environment.

Stable isotope analysis provides ecologists with a new type of "lens" capable of revealing ecological relationships that would otherwise remain invisible. For example, ecologists using stable isotope analysis can track habitat use by American redstarts on their wintering grounds. In Jamaica, older male American redstarts, along with some females, spend the winter in higher-productivity mangrove forest habitats, pushing most females and younger males into poorer-quality, dry scrub habitat. The dominant plants in these two habitats and the insects that feed on them contain different proportions of the carbon isotopes ^{12}C and ^{13}C. Therefore, the tissues of the birds spending their winters in the productive mangrove habitat (lower ^{13}C) and those spending the winters in the poor scrub habitat (higher ^{13}C) are in effect chemically tagged. As a consequence, today's ecologist can analyze a very small sample of blood from an American redstart when it arrives on its temperate breeding ground and know the habitat where it spent the winter. When Ryan Norris and his research team made such measurements, they found that male redstarts that had spent the winter in the more productive mangrove habitat arrived on the breeding grounds earlier and produced significantly more young birds that survived to fledging.

Stable isotope analysis and the role that it has played in elucidating the ecology of a diversity of organisms will thread its way through the text. As is often the case in science, new tools create new research frontiers. Another of those frontiers is to be found in the canopies of forests.

Forest Canopy Research: A Physical and Scientific Frontier

Studies of warblers showcase how ecologists approach studies of one or a few species. Other ecologists have been concerned with the ecology of entire forests, lakes, or grasslands, which they treat as ecosystems. An **ecosystem** includes all the organisms that live in an area and the physical environment with which those organisms interact. Many ecosystem studies have focused on **nutrients,** the raw materials that an organism must acquire from the environment to live.

For ecologists who study the budgets of nutrients such as nitrogen, phosphorus, or calcium, one of the first steps is to inventory their distribution within an ecosystem. Inventories by Nalini Nadkarni (1981, 1984a, 1984b) changed our ideas of how tropical and temperate rain forests are structured and how they function. With the aid of mountain-climbing equipment, Nadkarni slowly made her first ascent into the canopy of the Costa Rican rain forest, a world explored by few others and where she was to become a pioneer (fig. 1.6). She stood on the rain forest floor and wondered about the diversity of organisms and ecological relationships that might be hidden in the canopy high above. Her wonder soon gave way to determination, and Nadkarni not only visited the canopy but was among the first to explore the ecology of this unseen world.

Because of leaching by heavy rains, many rain forest soils are poor in nutrients such as nitrogen and phosphorus. The low availability of nutrients in many rain forest soils has produced one of ecology's puzzles. How can the prodigious life of rain forests be maintained on such nutrient-poor soils? Many factors contribute to the maintenance of this intense biological activity. Nadkarni's research in the treetops uncovered one of those factors, a significant store of nutrients in the rain forest canopy.

The nutrient stores in the rain forest canopy are associated with epiphytes. **Epiphytes** are plants, such as many orchids and ferns, that live on the branches and trunks of other plants. Epiphytes are not parasitic: they do not derive their nutrition from the plant they grow on. As they grow on the branches of a tree they begin to trap organic matter, which eventually forms a mat. Epiphyte mats increase in thickness up to 30 cm, providing a complex structure that supports a diverse community of plants and animals.

Figure 1.6 Exploring the rain forest canopy. What Nalini Nadkarni discovered helped solve an ecological puzzle.

Epiphyte mats contain significant quantities of nutrients. Nadkarni estimated that these quantities in some tropical rain forests are equal to about half the nutrient content of the foliage of the canopy trees. In the temperate rain forests of the Olympic Peninsula in Washington, the mass of epiphytes is four times the mass of leaves on their host trees.

Nadkarni's research showed that in both temperate and tropical rain forests, trees access these nutrient stores by sending out roots from their trunks and branches high above the ground. These roots grow into the epiphyte mats and extract nutrients from them. As a consequence of this research, we now know that to understand the nutrient economy of rain forests the ecologist must venture into the treetops.

Easier means of working in the rain forest canopy have been developed, and this research is no longer limited to the adventurous and agile. New ways to access the forest canopy range from hot air balloons and aerial trams to large cranes. The Wind River Canopy Crane offers scientists access to any level within a 70 m tall coniferous forest in a 2.3 ha area near the Columbia River Gorge in Washington (fig. 1.7). Research projects supported—and made far easier—by this crane and others have included the ecology of migratory birds in the forest canopy, photosynthesis by epiphytes living at different canopy heights, and vertical stratification of habitat use by bats and beetles (Ozanne et al. 2003). By 2006, there were 12 canopy cranes facilitating canopy research in temperate and tropical forests worldwide (Stork 2007). Nadkarni points

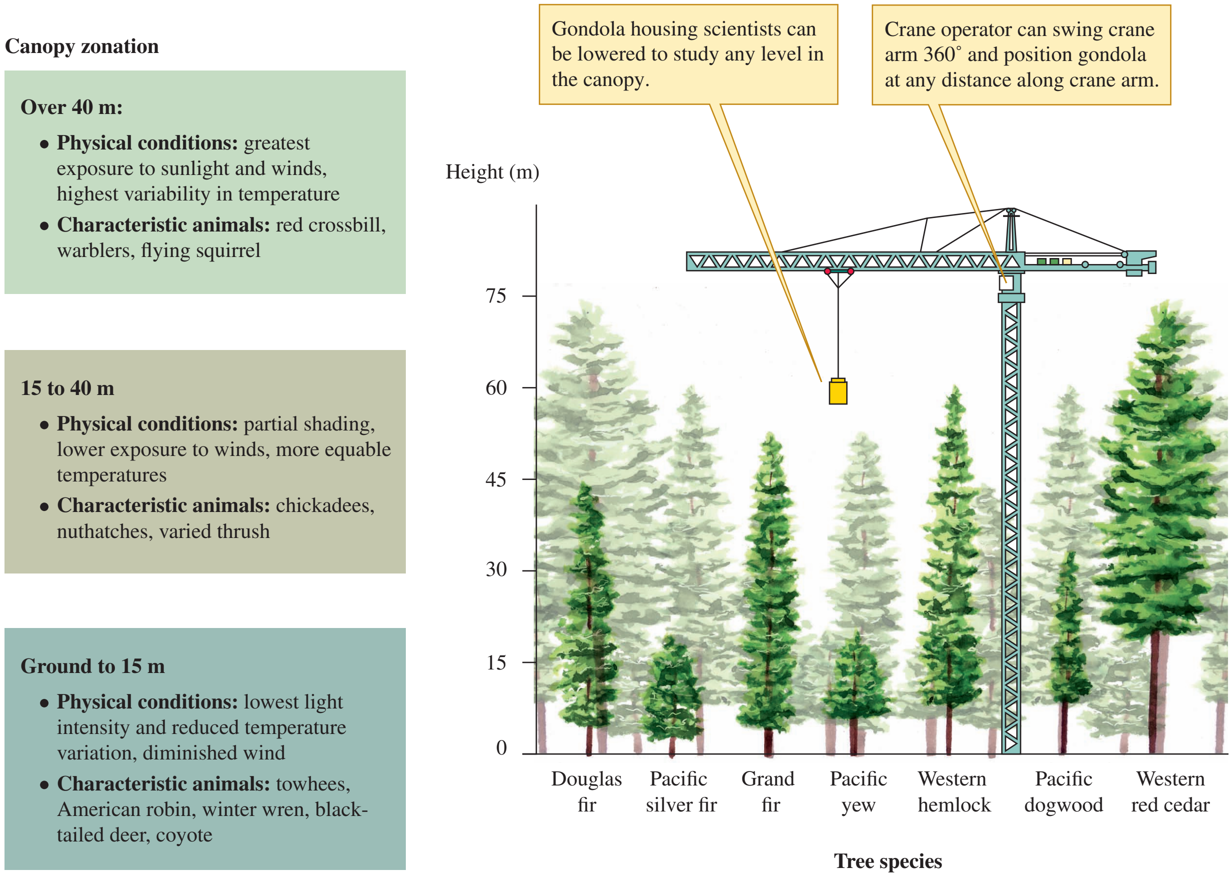


Figure 1.7 The Wind River Canopy Crane provides access to the forest canopy for a broad range of ecology and ecological studies.

out, in response to these developments, that the canopy as a physical frontier may be closing, but its exploration as a scientific frontier is just beginning, particularly as we attempt to predict the ecological consequences of climate change.

Climatic and Ecological Change: Past and Future

The earth and its life are always changing. However, many of the most important changes occur over such long periods of time or at such large spatial scales that they are difficult to study. Two approaches that provide insights into long-term and large-scale processes are studies of pollen preserved in lake sediments and evolutionary studies.

Margaret Davis (1983, 1989) carefully searched through a sample of lake sediments for pollen. The sediments had come from a lake in the Appalachian Mountains, and the pollen they contained would help her document changes in the community of plants living near the lake during the past several thousand years. Davis is a paleoecologist trained to think at very large spatial scales and over very long periods of time. She has spent much of her professional career studying changes in the distributions of plants during the Quaternary period, particularly during the most recent 20,000 years.

Some of the pollen produced by plants that live near a lake falls on the lake surface, sinks, and becomes trapped in lake sediments. As lake sediments build up over the centuries, this pollen is preserved and forms a historical record of the kinds of plants that lived nearby. As the lakeside vegetation changes, the mix of pollen preserved in the lake's sediments also changes. In the example shown in figure 1.8, pollen from spruce trees, *Picea* spp., first appears in lake sediments about 12,000 years ago then pollen from beech, *Fagus grandifolia,* occurs in the sediments beginning about 8,000 years ago. Chestnut pollen does not appear in the sediments until about 2,000 years ago. The pollen from all three tree species continues in the sediment record until about 1920, when chestnut blight killed most of the chestnut trees in the vicinity of the lake. Thus, the pollen preserved in the sediments of lakes can be used to reconstruct the history of vegetation in the area. Margaret B. Davis, Ruth G. Shaw, and Julie R. Etterson review extensive evidence that during climate change, plants evolve, as well as disperse (Davis and Shaw 2001; Davis, Shaw, and Etterson 2005). As climate changes, plant populations simultaneously change their geographic distributions and undergo the evolutionary process of **adaptation,** which increases their ability to live in the new climatic regime. Meanwhile, evidence of evolutionary responses to climate change is being discovered among many animal groups. William Bradshaw and Christina Holzapfel (2006) summarized several studies documenting evolutionary change in northern animals,

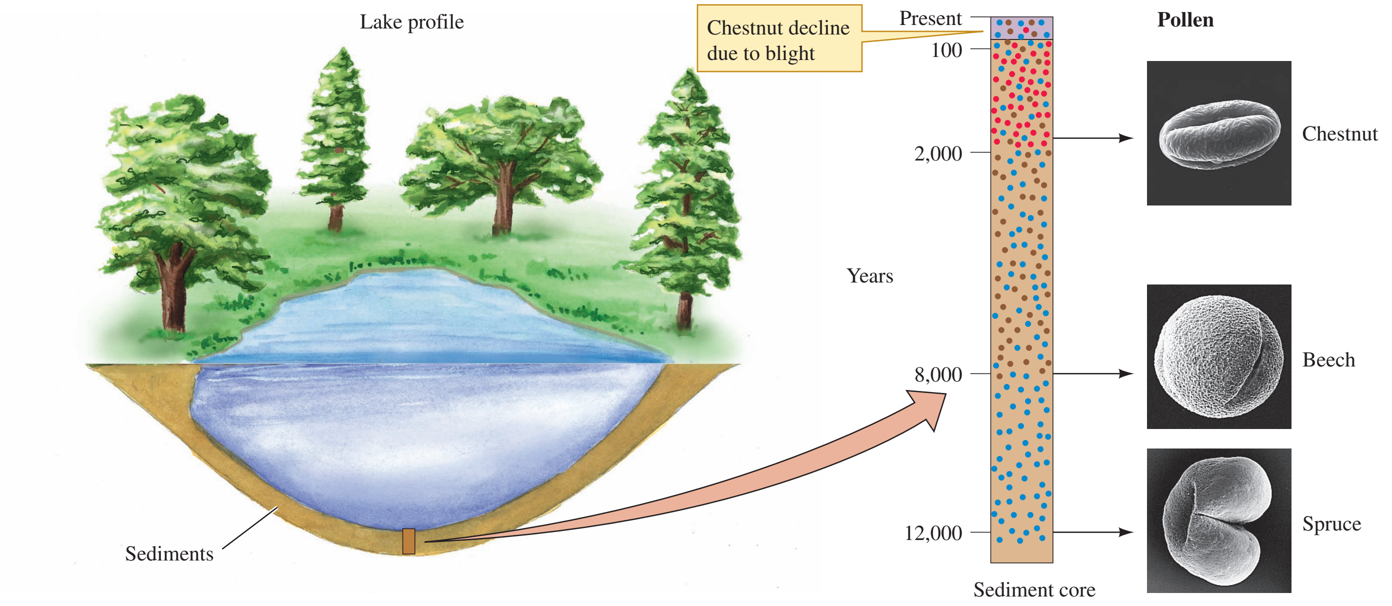


Figure 1.8 The vegetation history of landscapes can be reconstructed using the pollen contained within the sediments of nearby lakes.

ranging from small mammals and birds to insects (fig. 1.9), in response to increasing growing season length as a consequence of the now-well-documented phenomenon of global warming (see chapter 23, p. 519). Research such as that by Davis and her colleagues will be essential to predicting and understanding ecological responses to global climate change.

Figure 1.9 Studies indicate that north American red squirrels, *Tamiasciurus hudsonicus,* have been undergoing rapid evolution for earlier breeding, during a recent period of increased average spring temperatures in Canada's Yukon Territory (Réale et al. 2003).

In the remainder of this book we will fill in the details of the sketch of ecology presented in this chapter. This brief survey has only hinted at the conceptual basis for the research described. Throughout this book we emphasize the conceptual foundations of ecology. Each chapter focuses on a few ecological concepts. We also explore some of the applications associated with the concepts introduced. Of course, the most important conceptual tool used by ecologists is the scientific method, which is introduced on page 9.

We continue our exploration of ecology in section I with natural history and evolution. Natural history is the foundation on which ecologists build modern ecology for which evolution provides a conceptual framework. A major premise of this book is that knowledge of natural history and evolution improves our understanding of ecological relationships.

Concept 1.2 Review

1. How were the warbler studies of Robert MacArthur and those that focused on the American redstart similar? How did they differ?
2. What aspects of Nalini Nadkarni's research identify it as "ecosystem ecology"? Give examples of research in forest canopies that would address other levels of ecological organization (for examples, see fig. 1.1).
3. The discussion of the research by Margaret Davis and her colleagues did not identify the questions that they addressed. What research questions can we infer from the above description of their work?

✓ **Information**
Hypothesis
Predictions
Testing

Investigating the Evidence 1

The Scientific Method–Questions and Hypotheses

LEARNING OUTCOMES

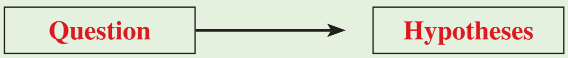
After studying this section you should be able to do the following:

1.8 Distinguish between questions and hypotheses in the scientific process.

1.9 Discuss the scientific method, emphasizing hypothesis testing.

Ecologists explore the relationships between organisms and environment using the methods of science. The series of boxes called "Investigating the Evidence" that are found throughout the chapters of this book discuss various aspects of the scientific method and its application to ecology. While each box describes only a small part of science, taken together, they represent a substantial introduction to the philosophy, techniques, and practice of ecological science.

Let us begin this distributed discussion with the most basic point. What is science? The word *science* comes from a Latin word meaning "to know." Broadly speaking, science is a way of obtaining knowledge about the natural world using certain formal procedures. Those procedures, which make up what we call "the scientific method," are outlined in figure 1. Despite a great diversity of approaches to doing science, sound scientific studies have many methodological characteristics in common. The most universal and critical aspects of the scientific method are: asking interesting questions and forming testable hypotheses.



Questions and Hypotheses

What do scientists do? Simply put, scientists ask and attempt to find answers to questions about the natural world. Questions are the guiding lights of the scientific process. Without them, exploration of nature lacks focus and yields little understanding of the world. Let's consider a question asked by an ecologist discussed in this chapter. The main question asked by Robert MacArthur in his studies of warblers (p. 4) was something like the following: "How can several species of insect-eating warblers live in the same forest without one species eventually excluding the others through competition?" While this focus on questions may seem obvious, one of the most common questions asked of scientists at seminars and professional meetings is, "What is your question?"

If scientists are in the business of asking questions about nature, where does a hypothesis enter the process?

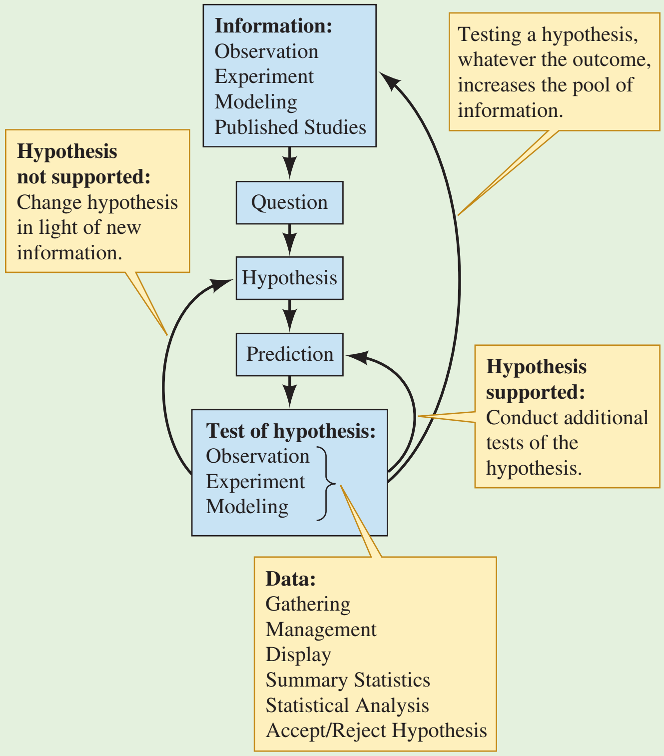


Figure 1 Graphic summary of the scientific method. The scientific method centers on the use of information to propose and test hypotheses through observation, experiment, and modeling.

A hypothesis is a possible answer to a question. MacArthur's main hypothesis (possible answer to his question) was: "Several warbler species are able to coexist because each species feeds on insects living in different zones within trees."

Once a scientist or team of scientists proposes a hypothesis (or multiple alternative hypotheses), the next step in the scientific method is to determine its validity by testing predictions that follow from the hypothesis. Three fundamental ways to test hypotheses are through observation, experiments, and modeling. These approaches, which are all represented in figure 1, will be discussed in detail in the "Investigating the Evidence" boxes and in the research discussed in later chapters.

Critiquing the Evidence 1

1. How does the development of new research tools, such as canopy cranes and stable isotope analysis, affect the process of science as outlined by figure 1 of this "Investigating the Evidence" box?