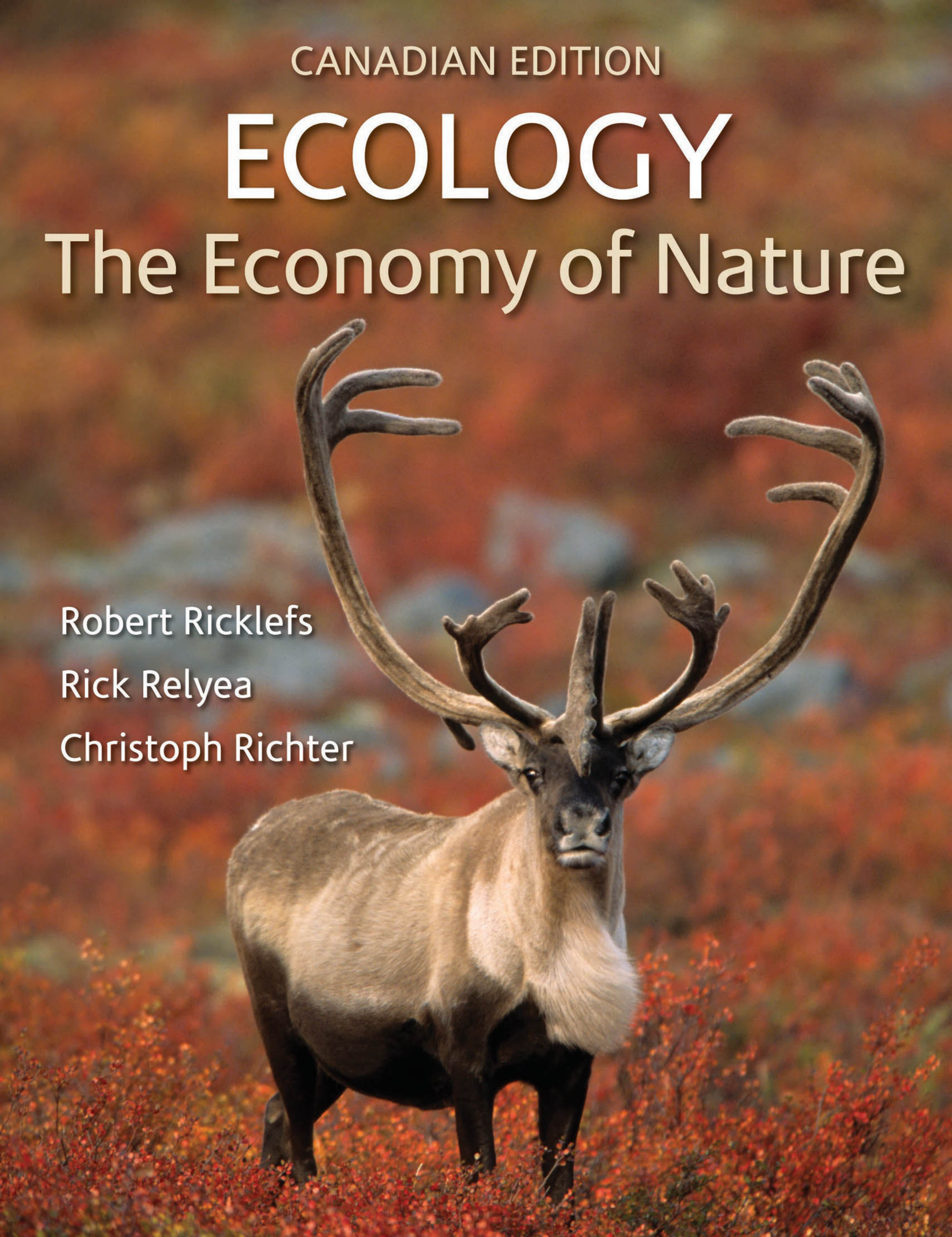
CANADIAN EDITION

ECOLOGY
The Economy of Nature



Robert Ricklefs
Rick Relyea
Christoph Richter

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Canadian Edition

Ecology

The Economy of Nature

Seventh Edition

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University of Missouri–St. Louis

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University of Toronto–Mississauga

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ABOUT THE AUTHORS


Photo by Maria W. Pil

ROBERT RICKLEFS is Curators' Professor of Biology at the University of Missouri–St. Louis, where he has been a member of the faculty since 1995. His teaching at Missouri, and previously at the University of Pennsylvania, has included courses in introductory and advanced ecology, biogeography, evolution, and biological statistics. Bob's research has addressed a broad range of topics in ecology and evolutionary biology, from the adaptive significance of life-history traits of birds, to island biogeography and the community relationships of birds, herbivorous insects, and forest trees. In particular, he has championed the importance of recognizing the impact of large-scale processes on local ecological assemblages of species. Bob has published in numerous journals including *Science, Nature, PNAS, Evolution, Ecology, Ecology Letters,* and the *American Naturalist*. His contributions have been recognized by honorary doctorates from the Université Catholique de Louvain (Belgium), Aarhus University (Denmark), and the University of Burgundy (France). He is a member of the American Academy of Arts and Sciences and the National Academy of Sciences of the United States. Bob published the first edition of *The Economy of Nature* in 1976 and is joined by a coauthor for the first time with this seventh edition.


Photo by Christine Relyea

RICK RELYEA is Professor of Biology at the University of Pittsburgh, where he has been on the faculty since 1999. In 2005 he was named the Chancellor's Distinguished Researcher at the University of Pittsburgh, and he was the 2014 recipient of the David and Tina Bellet Teaching Excellence Award. Since 2007, he has also served as the director of the University of Pittsburgh's field station, the Pymatuning Laboratory of Ecology, where he oversees a diverse set of ecological field courses and facilitates researchers from around the world. Rick has taught thousands of undergraduate students in introductory ecology, behavioural ecology, and evolution. His research is recognized throughout the world and has been published in the leading ecological journals including *Ecology, Ecology Letters, American Naturalist,* and *PNAS*. The research spans a wide range of ecological and evolutionary topics including animal behaviour, sexual selection, ecotoxicology, disease ecology, phenotypic plasticity, community ecology, ecosystem ecology, and landscape ecology. Rick's research focuses on aquatic habitats and the diversity of species that live in these ecosystems. He strives to integrate different areas of ecology in ways that provide new discoveries and applications.


Photo by Silvia Caicedo

CHRISTOPH RICHTER is Lecturer in the Department of Biology at the University of Toronto–Mississauga, where he has been on the faculty since 2011. He began his teaching career in 2002 at Queen's University, where he was recognized for his excellence in teaching. He has taught undergraduate courses on many topics including introductory ecology, animal behaviour, vertebrate biology, marine mammalogy, biological diversity, and statistics. He strives to engage students by making course content relevant for them and by demonstrating the dynamic nature of scientific research. His teaching has taken him from the Arctic to the Gulf of Maine and to Ecuador. Christoph earned a MSc from Memorial University of Newfoundland and a PhD from Otago University in New Zealand. His research focused on the impacts of human activities, such as fishing, whale watching, and oil exploration, on the behaviour of cetaceans. Christoph's current research focuses on students' opinions and knowledge of evolutionary concepts and on factors that limit academic success. He is also interested in involving undergraduate students in collecting and using long-term ecological data sets.

PREFACE

From the Authors…

Since *The Economy of Nature* debuted in 1976, it has enjoyed a strong and loyal following. This edition, the seventh, begins a new collaboration. When we first talked about the book in 2009, it was immediately clear that we had a similar vision to retain everything instructors loved while updating it for today's instructors and students, and to make it as relevant as possible for students and instructors across Canada. We asked hundreds of ecology instructors what they want to see in a textbook and we listened carefully to the challenges they face. We thought about ways to make Canadian students connect more deeply with the material and how we might bring the Canadian context to bear on many of the ecological issues important to Canadians today. You hold in your hands the result of a five-year effort to bring an exciting and completely new textbook to you and your students.

A new vision.

Chapters are organized around four to six key concepts that are repeated as major headings and repeated again in streamlined summaries. This new structure allows the instructor and student to focus on the essential messages of each chapter.

The chapters contain substantially *more figures showing real data with a better balance between terrestrial and aquatic systems*. These changes will give students more experience in seeing and interpreting scientific data from a wide range of systems. We have also increased our coverage of species interactions, community ecology, and ecosystem ecology to provide a broader scope for an introductory course.

You told us that you want ecological applications integrated throughout the entire book rather than relegated to a final chapter. We agree, *so every chapter now contains multiple studies with real-world applications that underscore the value of understanding ecology and that help students understand why ecology is relevant to their lives*.

Like you, we strive to include global change throughout our ecology course. To make this possible, we now *discuss global change issues in nearly every chapter*. These changes help instructors and students make the connections between basic ecology and real ecological issues that affect their lives.

We know that students appreciate clear writing and strong visuals. To make the text an appealing study tool that students will want to read, we worked with superb editors who helped us put *the science into plain language without diminishing the complexity of the concepts*. We have also replaced nearly every photo, graph, and illustration in the book. We now give you and your students *an abundance of spectacular photos, beautiful color illustrations, and easy-to-interpret graphs*.

Presents the process of scientific discovery through a global lens.

As active researchers ourselves, we want students to know that science is an ongoing process. In every chapter *we show students how scientists begin with hypotheses and test them* *with data that the students can view and interpret*. We demonstrate how early hypotheses are continually revised as new observations and new data are produced. To help convey the dynamic nature of ecology to your students, *we have retained all of your favorite classic studies while adding a large number of new, captivating studies from around the world,* including many from 2010 to 2013.

Takes a learning-by-doing approach to basic quantitative tools and the use of data.

You have told us that many of today's students lack the background to apply basic quantitative tools. This edition contains a new feature, "Analyzing Ecology," *to help students learn basic statistical and mathematical techniques that real ecologists use every day*. We show students how to do the math and then challenge them to apply it in "Your Turn." We make a point of integrating these tools with research studies that are discussed in the chapters.

To help students gain more practice with quantitative skills, we created a feature at the end of each chapter, "Practicing Ecology," in which *students are challenged to understand how to create and interpret different types of graphs*. To provide immediate feedback to students, answers to both "Analyzing Ecology" and "Practicing Ecology" exercises are provided at the back of the book.

Considers many scales and diverse habitats.

To make the seventh edition reflect the broad range of modern ecology, *we have included examples from a wider diversity of organisms—from microbes to vertebrates*. The section on species interactions includes new chapters on mutualism and parasitism to reflect the importance of these interactions in ecological communities. The research examples also come from a diversity of terrestrial and aquatic habitats.

Fosters ecological literacy through environmental applications.

As ecology instructors, we want to make the material interesting and relevant to our students—most of whom will not go on to become professional ecologists. *Our addition of hundreds of applied studies demonstrates the relevance of ecology in students' lives*. Every chapter now opens with an attention-grabbing case study that highlights important and relevant research to pique student interest. Chapters end with an application called *Ecology Today: Connecting the Concepts*—examples of applied ecology that bring together the major concepts of the chapter and demonstrate their practical importance in a variety of arenas including human health, conservation, and managing our environment.

While making all of these improvements, we were committed to *streamlining the book from 27 to 23 chapters, so it will be more manageable for a one-semester course*. Our goal is to give you a text that presents the material most relevant to class lectures, discussions, and activities. Based on feedback from hundreds of ecology instructors whom we asked to read the chapters, there is broad agreement that this new edition is a beautiful book that will intrigue your students and capture their interest. We look forward to hearing from you as you review the book and we encourage you to share your thoughts with us.

Robert Ricklefs Rick Relyea Christoph Richter

Acknowledgments

We were incredibly fortunate to work with a tremendous group of people who made this new edition possible. As with every textbook, each chapter began with a text manuscript and an art manuscript that moved through many revisions to make the final version clear and interesting to undergraduate students. We had the privilege of working daily with developmental editor Rebecca Kohn and art editor Lee Wilcox. These two individuals played a major role in dramatically revising this new edition. Aaron Stoler was instrumental in bringing our vision for the "Practicing Ecology" feature to the page. Claire Hunter handled all the reviewing and surveys and conducted focus groups on the text's design. Other individuals who played key roles in the book's success include senior acquisitions editor Bill Minick, project editor Elizabeth Geller, copy editor Fred Burns, art director Diana Blume, and production manager Susan Wein. Our replacement of nearly every photograph, graph, and illustration required a tremendous effort by a spectacular team; MGMT produced beautiful graphs, Nicolle Fuller of Sayo Art produced stunning illustrations, and the team of Deborah Goodsite and Christine Buese were tireless in hunting down just the right photo to meet each of our requests.

During the past six editions, countless colleagues and instructors have helped shape *Ecology: The Economy of Nature* into a book that has introduced tens of thousands of students to the wonders of ecology. We are extremely grateful to these colleagues. As we undertook a major revision with this seventh edition, we once again received extensive help at every stage of development from many of our colleagues and fellow instructors. We extend our sincere thanks to the following people who graciously offered their time:

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Lan Xu, *South Dakota State University*
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Teaching in a Canadian Context

Uniquely Canadian Examples

ECOLOGY The Economy of Nature, Canadian Edition has been created to meet the needs of instructors teaching the basic ecology course to biology students in a Canadian context. It is filled with relevant Canadian case studies, photos, and graphics.

The following is a list of some of the uniquely Canadian examples and case studies covered in the text.

Chapter 2 Adaptations to Aquatic Environments

- Example of limestone sediments, Figure 2.8: *Percé Rock, Gaspe Peninsula*, Quebec.
- Example of thermophiles, Figure 2.19: *Rabbitkettle Hotsprings, Yukon*.
- Migration of salmon on *Fraser River* affected by water temperatures.

Chapter 3 Adaptations to Terrestrial Environments

- Examples of structural adaptations of plants against heat and drought, Figure 3.13: Native Canadian species.
- Example of basking, Figure 3.19: Five-lined skink.
- Example of counter-current circulation, Figure 3.22: Caribou.

Chapter 4 Adaptations to Variable Environments

- Examples of spatial variation, Figure 4.2: Various locations across Canada.
- Adaptations to fluctuating salt environments, Figure 4.12: *Vancouver Island, British Columbia*.
- Adaptability of food choices in sea otters living off the coast of *Newfoundland*.

Chapter 5 Climates and Soils

- Hardiness zones for plants across Canada, chapter opener and map.
- Example of regressions, using Canada temperature information, "Analyzing Ecology."
- Example of rainshadow, the prairie in *southern Alberta*.
- Inclusion of Ae soil horizon, Figures 5.16 and 5.17.
- Polar bears in *Labrador*.

Chapter 6 Terrestrial and Aquatic Biomes

- Climate diagram examples:
  - Figure 6.5, Tundra biome: *Iqaluit, Nunavut*
  - Figure 6.6, Boreal forest biome: *Whitehorse, Yukon*
  - Figure 6.7, Temperate rainforest biome: *Carmanah Point, British Columbia*
  - Figure 6.10, Temperate grassland/cold desert biome: *Brandon, Manitoba*
- Example of a river, Figure 6.14: *Athabasca River, Alberta*
- Example of a lake, Figure 6.14: *Lake Louise, Alberta*
- Examples of freshwater wetlands, Figure 6.17: Swamp in *Campbellville, Ontario*.
- Marsh in *Point Pelee, National Park in Leamington, Ontario*; bog in the *Mingan Archipelago National Park Reserve in Quebec*.
- Example of salt marsh, Figure 6.18: *Prince Edward Island*.
- Examples of intertidal zones, Figure 6.20: *Gros Mornee National Park, Newfoundland and Labrador, and Bay of Fundy, New Brunswick*.

Chapter 7 Evolution and Adaptation

- Example of evolution through selection, Figures 7.4 and 7.5: Spirit bears on coast of *British Columbia*.
- Example of bottleneck effect, Figure 7.7: Whooping crane
- Case study on founder effect: Founder effect in the *Saguenay–Lac-Saint-Jean region of northeastern Quebec*.
- Case study on sympatric speciation, Figure 7.19: Stickleback species living in some of *British Columbia's coastal lakes*.
- Case study on drug resistant tuberculosis in Inuit communities.

Chapter 8 Life Histories

- Case study on offspring number versus offspring size: Salmon in *Nova Scotia*.
- Case study on comparisons within species: Pumpkinseed sunfish in *Ontario lakes*.
- Canadian data on senescence in humans, Figure 8.11.
- Case study on Canadian fisheries with regard to life history and commercial fishing.

Chapter 9 Reproductive Strategies

- Example of a Canadian plant that uses vegetative reproduction, Figure 9.1: Arctic Ross's sandwort.
- Case study on adaptive sex determination, Figure 9.10: Atlantic silverside fish.
- Example of sexual dimorphism among caribou, Figure 9.17.

- Case study of sexual conflict among water striders, Figure 9.21

Chapter 10 Social Behaviours

Case study on competition among killer whales off the coast of *British Columbia*, Figure 10.5

Chapter 11 Population Distributions

- Case study on distribution of horse gentian showing how small-scale variation in the environment can create geographic ranges that are composed of small patches of suitable habitat, Figure 11.2
- Case study on suitability of habitat using four species of moss in *Alberta peatland*, Figure 11.3
- Case study of the geographic range of the red-winged blackbird throughout Canada, Figure 11.6
- Discussion of *Yukon Territory to Yellowstone corridor*, Figure 11.15.

Chapter 12 Population Growth and Regulation

- Case study of growth in sea otter population in *British Columbia* waters.
- Case study of negative density dependence in deer mouse population in *Algonquin Park, Ontario*, Figure 12.8.

Chapter 13 Population Dynamics over Space and Time

- Case study of wolverine hunt in Canada as a measure of population size, Figure 13.1
- Dating the ages of existing trees in an *old-growth forest in Manitoba* to determine how age structures of populations changed over time, Figure 13.4
- Case study of duck populations on three *archipelagos off the Labrador coast* to examine extinction in small populations, Figure 13.13.
- Case study on a metapopulation of the Rocky Mountain Parnassian butterfly in meadows on the eastern slopes of the Canadian Rocky Mountains to discuss the importance of patch size and patch isolation, Figure 13.19.

Chapter 14 Predation and Herbivory

- Case study on the effects of herbivores, fencing out deer in *Gwaii Haanas National Park Preserve and Heritage Site, British Columbia*, Figure 14.6.
- Case study on plant response to herbivory, the lesser snow goose in the *wetlands of Hudson Bay Lowlands.*

Chapter 15 Parasitism and Infectious Disease

- Case study on Dutch Elm disease in *Toronto*.
- Case study on SARS in *Toronto*.
- Discussion of Lyme disease in Canada.

Chapter 16 Competition

- Competition for space on *Whaler Islets off the coast of Vancouver Island, British Columbia,* Figure 16.1.
- Case study on competition among mosses in *northeastern Alberta*.
- Case study on disturbances and competition in *fescue prairie in Alberta and Saskatchewan,* Figure 16.11.
- Case study on herbivory and plants with tent caterpillars and trembling aspens in *Alberta*.
- Case study on apparent competition and variation over time with woodland caribou, wolves, and moose, west of the *Athabasca River in northeastern Alberta*, Figure 16.18.

Chapter 17 Mutualism

- Case study on the mutualistic relationship between grasses and their arbuscular mycorrhizal fungi in *Grassland National Park, Saskatchewan*.
- Case study on how a change in fungal abundance might affect plant and insect communities in an *Alberta grassland*, Figure 17.21.
- Case study on how communities are also influenced by the responses of different plant species to arbuscular mycorrhizal fungi, discussion of an experiment carried out at Guelph University.

Chapter 18 Community Structure

- Changes in vegetation as one walks from the base to the top of a *mountain on the eastern side of the Rocky Mountains in Alberta*, Figure 18.1
- Case study on recolonization after fire of areas in the *boreal mixed-wood forest in Alberta*.
- Case study on distribution of fish abundance based on survey from Canada's Department of Fisheries and Oceans, Figure 18.8.
- Case study of how a community can move to an alternative stable state in the lichen woodlands in *Quebec's Parc des Grands-Jardins*.

Chapter 19 Community Succession and Development

- Succession at *Hudson Bay*, Figure 19.2
- Case study on observed changes in the animal community that coincide with plant succession in the black spruce forests in *western Quebec*.
- Discussion of succession in the *Saint Lawrence estuary*.
- Persistence of fire-tolerant species in the *Yukon Territory*.
- Case study of how intense grazing by greater snow geese reduces dominant grass species, Figure 19.17.

Chapter 20 Movement of Energy in Ecosystems

- Case study on invasive species and food web alteration with worms introduced into the forests of the *Kananaskis Valley in Alberta*.
- General patterns in the distribution of primary productivity across Canada, Figure 20.6.

Chapter 21 Movement of Elements in Ecosystems

- Dead zone in the *lower St. Lawrence estuary in Quebec*.

- Natural Resources Canada study of ground water and aquifer use in Canada.
- Canada limits the use of phosphorus in detergents.
- Nutrient travel in *streams in British Columbia*.

Chapter 22 Landscape Ecology, Biogeography, and Global Biodiversity

- Case study on causes of habitat heterogeneity in the *boreal forest of the Lake Nipigon region in northwestern Ontario*, Figure 22.2.
- An example of legacy effects, *an esker near Whitefish Lake, Northwest Territories*, Figure 22.1.
- Case study on relationship between habitat heterogeneity and species diversity among bird species in the *boreal forest of Alberta*.
- Case study of marbled murrelet threatened by increasing edge habitat in old growth forests on the *British Columbia coast*, Figure 22.10.
- Case study on matrix of habitats between fragments with Alpine Parnassius butterfly on the *eastern slopes of the Rocky Mountains in Alberta*.

Chapter 23 Global Conservation

- Economic benefit of boreal forests in Canada.
- Variety in Canadian apple farming as an example of declining agricultural diversity.
- Reduction in the amount of old-growth forest in Canada.
- Loss of *tallgrass prairie in Manitoba*.
- Restriction on DDT use in Canada.
- Case study on conservation in *Wood Buffalo National Park, in Alberta and the Northwest Territories*, Figure 23.22.

Focus on Canadian Research: Practicing Ecology

The “Practicing Ecology” feature highlights the work of researchers in Canada. These extended problems give students the opportunity to work with real data, build graphs, and think critically to interpret experimental results.

Chapter 2 Adaptations to Aquatic Environments

Seeing Underwater Shai Sabbah and his colleagues from Queen’s University investigate how the visual system of fish is adapted to light transmission underwater.

Chapter 3 Adaptations to Terrestrial Environments

Habitat Choices of Lizards Stephen Lougheed and his lab at Queen’s University have been studying how skinks cope with extreme temperatures.

Chapter 4 Adaptations to Variable Environments

Plastic Mouths in Fish Dolph Schluter and his colleagues at the University of British Columbia have studied the morphological plasticity of fish mouths in response to changing prey abundances.

Chapter 5 Climates and Soils

Why Are the Polar Bears Disappearing? Ian Stirling and his colleagues from Environment Canada have examined possible reasons why polar bear populations have declined in recent years.

Chapter 6 Terrestrial and Aquatic Biomes

Methane Production in Peatlands Tim Moore, from McGill University, and his colleagues have studied how changes in precipitation influence the decomposition of peat.

Chapter 7 Evolution and Adaptation

Predator Preferences and Prey Phenotypes Elizabeth Boulding and her lab at the University of Guelph study the response of phenotypes to selection in intertidal and marine environments.

Chapter 8 Life Histories

Trophy Hunting for Bighorn Sheep David Coltman from the University of Alberta and his colleagues have studied how sport hunting has altered the evolutionary trajectory of bighorn rams.

Chapter 9 Reproductive Strategies

How to Handle Sneaky Males Bryan Neff and his lab from the University of Western Ontario study behavioural ecology and the evolution of mating systems.

Chapter 10 Social Behaviours

Plants That Know Their Kin As a researcher at the University of Toronto, Jay Biernaskie studied the fitness consequences of kin recognition in plants.

Chapter 11 Population Distributions

Blowing Across the Geographic Range Chris Eckert and his lab at Queen’s University in Ontario study evolutionary adaptations that enable plants to disperse across a landscape.

Chapter 12 Population Growth and Regulation

Acidification and Zooplankton Shelley Arnott from Queen’s University and her colleagues study the factors that determine the distribution and abundance of freshwater invertebrates.

Chapter 13 Population Dynamics over Space and Time

Voles and Berries Charles Krebs at the University of British Columbia and his colleagues study the causes and consequences of rodent population fluctuations in North American forests.

Chapter 14 Predation and Herbivory

Indirect Effects of Deer Herbivory Peter Arcese from the University of British Columbia and his colleagues study the effects of animal management and conservation on ecosystems.

Chapter 15 Parasitism and Infectious Disease

The Cost of Having a Bodyguard Jacques Brodeur from Université de Montréal and his colleagues study interactions between herbivores and their enemies.

Chapter 16 Competition

The Importance of Diversity Marc Cadotte at the University of Toronto studies how plant diversity alters competition and primary productivity.

Chapter 17 Mutualism

The Benefits of a Backup Plan Megan Frederickson at the University of Toronto studies the factors that maintain mutualistic relationships between plants and animals.

Chapter 18 Community Structure

Invasive Crayfish and Trophic Cascades Jonathan Moore at Simon Fraser University studies how the invasion or extinction of species alters the functioning of aquatic ecosystems.

Chapter 19 Community Succession and Development

Determining Conservation Baselines Mark Vellend and his lab at the Université de Sherbrooke study the historical and contemporary processes that alter plant communities.

Chapter 20 Movement of Energy in Ecosystems

Viruses and Marine Nutrient Cycling Chris Suttle and his lab at the University of British Columbia study the ecological importance of viruses in the open ocean.

Chapter 21 Movement of Elements in Ecosystems

Leaf after Death of Salmon John Richardson and his lab at the University of British Columbia study the factors that alter stream community composition and ecosystem function.

Chapter 22 Landscape Ecology, Biogeography, and Global Biodiversity

Maintaining Nightshade Nash Turley, a graduate student at the University of Toronto Mississauga, studies the ecology and conservation of plants and herbivorous insects.

Chapter 23 Global Conservation

A Critical Threshold for Cod Boris Worm at Dalhousie University in Nova Scotia studies global trends in marine conservation.

The seventh edition welcomes Rick Relyea and Christoph Richter.

Every chapter of *ECOLOGY The Economy of Nature,* Canadian edition has been restructured and rewritten to create an accessible, successful learning experience for a wide range of students.

Chapters are organized around four to six key concepts.

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An infected carpenter ant. In Thailand, carpenter ants that become infected by a fungus crawl down from the canopy and attach themselves to the underside of a leaf by biting the leaf vein and then dying. After death, a spore-producing stalk grows out of the ant's head and releases its spores into the environment. Photo by David Hughes/Penn State University.

canopy, its nest mates would remove the corpse before the fungus could grow the spore-producing structure that is critical to its reproduction.

The ability of parasites to act as puppet masters over the behaviour of their victims is just one way that parasites have evolved to improve their fitness. As we will discover in this chapter, parasites come in a wide variety of forms and their effects on hosts can range from mild to lethal. Adaptations that enable parasites to infect hosts and adaptions that help hosts to resist infections by parasites offer intriguing insights into the strategies of parasite–host interactions.

SOURCES: S. B. Andersen et al., The life of a dead ant: The expression of an adaptive extended phenotype, *American Naturalist* 174 (2009): 424–433.

D. P. Hughes et al., Behavioural mechanisms and morphological symptoms of zombie ants dying from fungal infection, *BMC Ecology* 11 (2011): 13.

T. Lefevre, and F. Thomas, Behind the scene, something else is pulling the strings: Emphasizing parasitic manipulation in vector-borne diseases, *Infection, Genetics and Evolution* 8 (2008): 504–519.

CHAPTER CONCEPTS

- Many different types of parasites affect the abundance of host species.
- Parasite and host dynamics are determined by the parasite's ability to infect the host.
- Parasite and host populations commonly fluctuate in regular cycles.
- Parasites have evolved offensive strategies while hosts have evolved defensive strategies.

The struggle between parasites and hosts has produced many fascinating examples of ecological interactions and evolutionary adaptations. In Chapter 1, we defined a parasite as an organism that lives in or on another organism, called the host, and causes harmful effects as it consumes resources from the host. Some hosts have **infection resistance**, which is the ability of a host to prevent the infection from occurring, while other hosts have **infection tolerance**, which is the ability of a host to minimize the harm that an infection can cause. The number of parasites of a given species that an individual host can harbour is known as the host's **parasite load**. A parasite typically has only one or a few species of hosts, although a given host could contain dozens of species of parasites. In fact, it is estimated that approximately half of all species on Earth are parasites.

When parasites cause an infectious disease, we call them *pathogens*. However, infection by a pathogen does not always result in a disease. For example, humans can be infected with human immunodeficiency virus (HIV) but they may never experience the disease symptoms known as Acquired Immune Deficiency Syndrome (AIDS). In many cases, it is not known what causes a host to transition from being infected by a pathogen to experiencing the disease.

Infectious diseases take a large toll on people; the World Health Organization estimates that more than 25 percent of all human deaths are caused by infectious diseases. Note that only infectious diseases are caused by pathogens; there are many noninfectious diseases in which pathogens do not play a role.

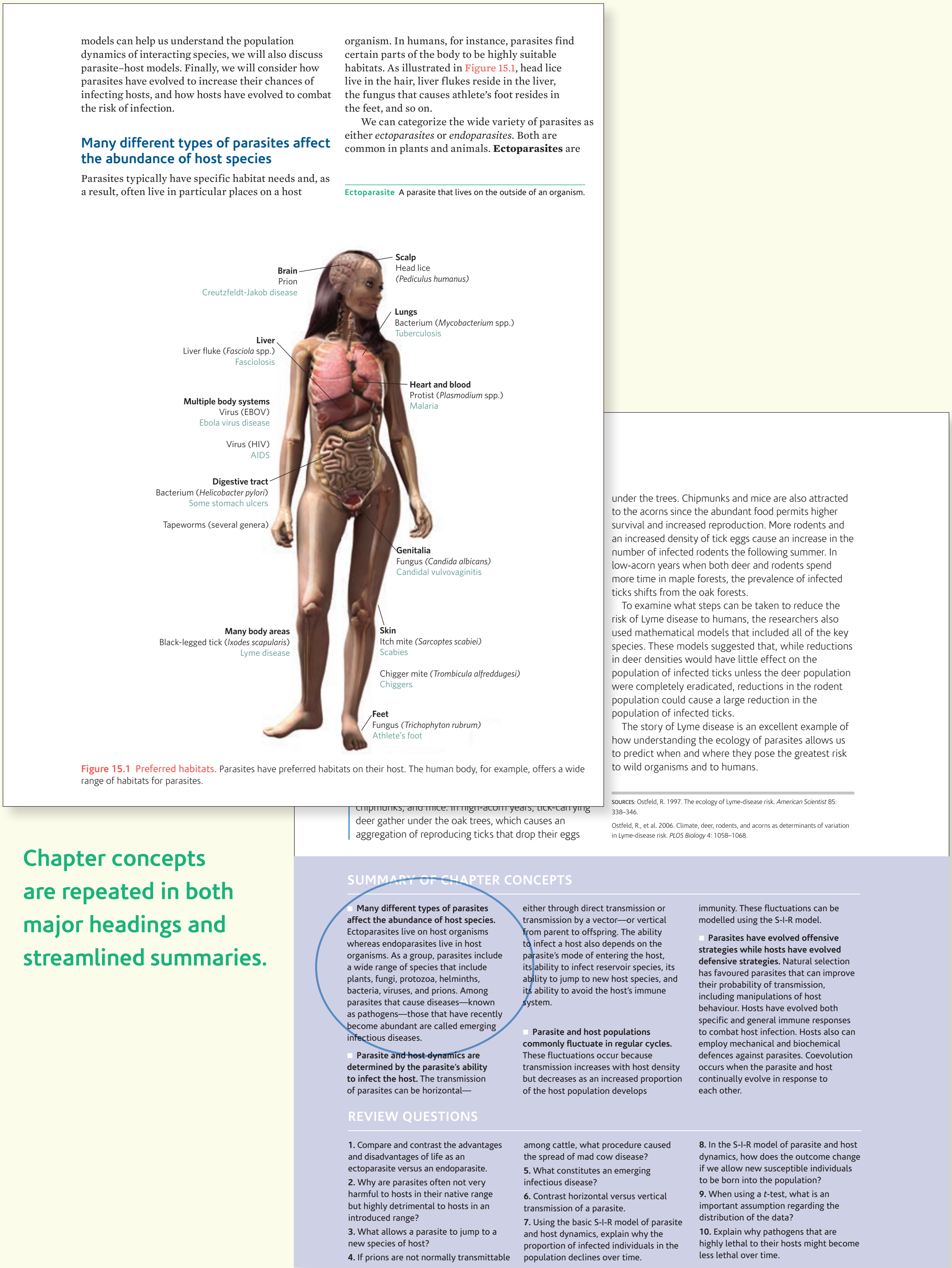
In this chapter, we will focus on the interaction between parasites and their hosts. In later chapters, we will discuss the larger role that parasites can play in communities and ecosystems. We will begin by looking at the many different types of parasites that exist, including those that have large effects on ecological communities, crops, domesticated animals, and human health. We will then examine the factors that determine whether parasites can infect hosts, spread rapidly through a population, and cause widespread harmful effects. Because mathematical

Infection resistance The ability of a host to prevent an infection from occurring.

Infection tolerance The ability of a host to minimize the harm that an infection can cause.

Parasite load The number of parasites of a given species that an individual host can harbour.

An organized learning experience.



models can help us understand the population dynamics of interacting species, we will also discuss parasite–host models. Finally, we will consider how parasites have evolved to increase their chances of infecting hosts, and how hosts have evolved to combat the risk of infection.

Many different types of parasites affect the abundance of host species

Parasites typically have specific habitat needs and, as a result, often live in particular places on a host organism. In humans, for instance, parasites find certain parts of the body to be highly suitable habitats. As illustrated in Figure 15.1, head lice live in the hair, liver flukes reside in the liver, the fungus that causes athlete's foot resides in the feet, and so on.

We can categorize the wide variety of parasites as either *ectoparasites* or *endoparasites*. Both are common in plants and animals. **Ectoparasites** are

Ectoparasite A parasite that lives on the outside of an organism.

Figure 15.1 Preferred habitats. Parasites have preferred habitats on their host. The human body, for example, offers a wide range of habitats for parasites.

under the trees. Chipmunks and mice are also attracted to the acorns since the abundant food permits higher survival and increased reproduction. More rodents and an increased density of tick eggs cause an increase in the number of infected rodents the following summer. In low-acorn years when both deer and rodents spend more time in maple forests, the prevalence of infected ticks shifts from the oak forests.

To examine what steps can be taken to reduce the risk of Lyme disease to humans, the researchers also used mathematical models that included all of the key species. These models suggested that, while reductions in deer densities would have little effect on the population of infected ticks unless the deer population were completely eradicated, reductions in the rodent population could cause a large reduction in the population of infected ticks.

The story of Lyme disease is an excellent example of how understanding the ecology of parasites allows us to predict when and where they pose the greatest risk to wild organisms and to humans.

SOURCES: Ostfeld, R. 1997. The ecology of Lyme-disease risk. *American Scientist* 85: 338–346.

Ostfeld, R., et al. 2006. Climate, deer, rodents, and acorns as determinants of variation in Lyme-disease risk. *PLOS Biology* 4: 1058–1068.

chipmunks, and mice. In high-acorn years, tick-carrying deer gather under the oak trees, which causes an aggregation of reproducing ticks that drop their eggs

SUMMARY OF CHAPTER CONCEPTS

- **Many different types of parasites affect the abundance of host species.** Ectoparasites live on host organisms whereas endoparasites live in host organisms. As a group, parasites include a wide range of species that include plants, fungi, protozoa, helminths, bacteria, viruses, and prions. Among parasites that cause diseases—known as pathogens—those that have recently become abundant are called emerging infectious diseases.
- **Parasite and host dynamics are determined by the parasite's ability to infect the host.** The transmission of parasites can be horizontal—either through direct transmission or transmission by a vector—or vertical from parent to offspring. The ability to infect a host also depends on the parasite's mode of entering the host, its ability to infect reservoir species, its ability to jump to new host species, and its ability to avoid the host's immune system.
- **Parasite and host populations commonly fluctuate in regular cycles.** These fluctuations occur because transmission increases with host density but decreases as an increased proportion of the host population develops immunity. These fluctuations can be modelled using the S-I-R model.
- **Parasites have evolved offensive strategies while hosts have evolved defensive strategies.** Natural selection has favoured parasites that can improve their probability of transmission, including manipulations of host behaviour. Hosts have evolved both specific and general immune responses to combat host infection. Hosts also can employ mechanical and biochemical defences against parasites. Coevolution occurs when the parasite and host continually evolve in response to each other.

REVIEW QUESTIONS

1. Compare and contrast the advantages and disadvantages of life as an ectoparasite versus an endoparasite.

2. Why are parasites often not very harmful to hosts in their native range but highly detrimental to hosts in an introduced range?

3. What allows a parasite to jump to a new species of host?

4. If prions are not normally transmittable among cattle, what procedure caused the spread of mad cow disease?

5. What constitutes an emerging infectious disease?

6. Contrast horizontal versus vertical transmission of a parasite.

7. Using the basic S-I-R model of parasite and host dynamics, explain why the proportion of infected individuals in the population declines over time.

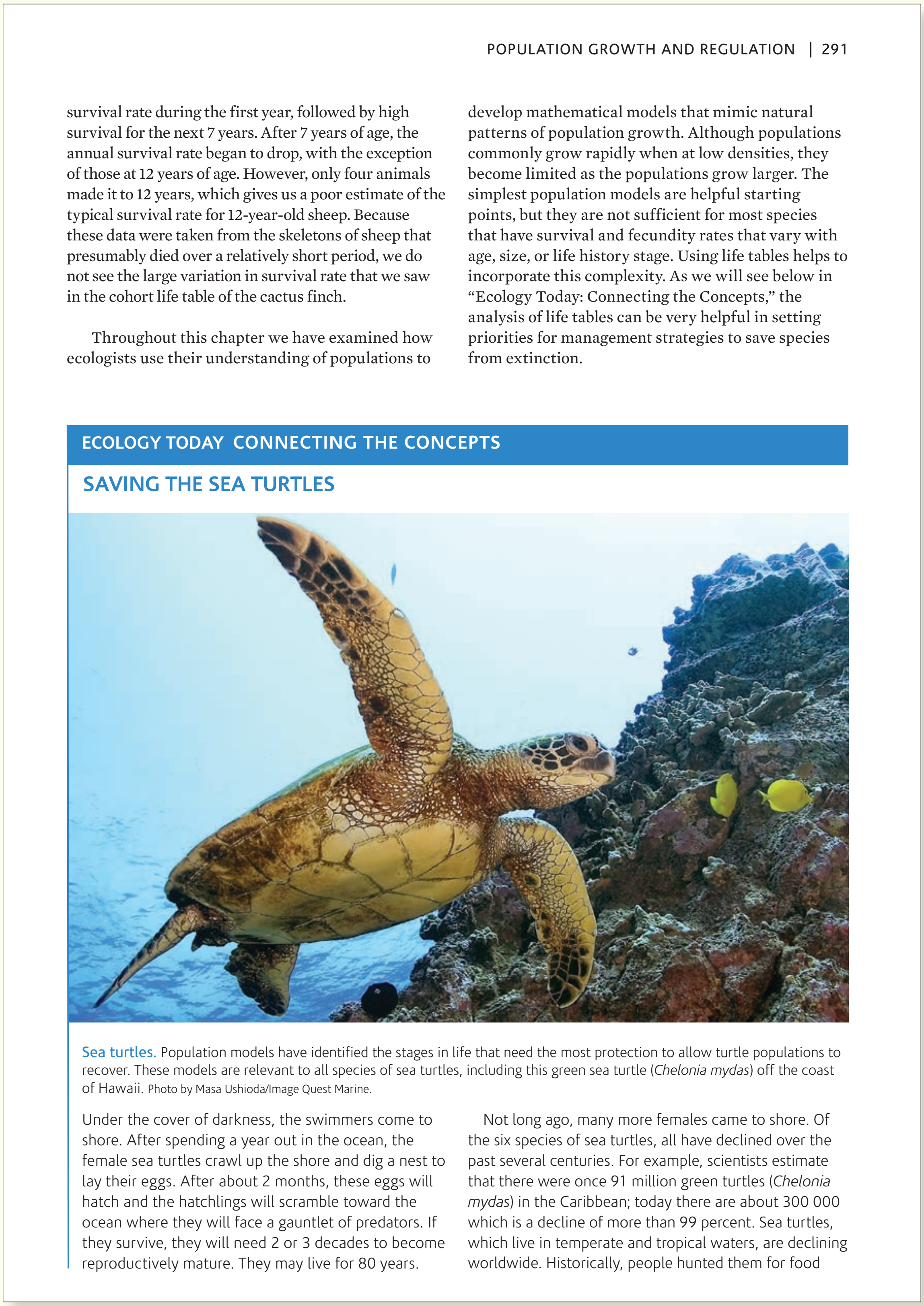
8. In the S-I-R model of parasite and host dynamics, how does the outcome change if we allow new susceptible individuals to be born into the population?

9. When using a *t*-test, what is an important assumption regarding the distribution of the data?

10. Explain why pathogens that are highly lethal to their hosts might become less lethal over time.

Chapter concepts are repeated in both major headings and streamlined summaries.

Hundreds of aquatic examples



POPULATION GROWTH AND REGULATION | 291

survival rate during the first year, followed by high survival for the next 7 years. After 7 years of age, the annual survival rate began to drop, with the exception of those at 12 years of age. However, only four animals made it to 12 years, which gives us a poor estimate of the typical survival rate for 12-year-old sheep. Because these data were taken from the skeletons of sheep that presumably died over a relatively short period, we do not see the large variation in survival rate that we saw in the cohort life table of the cactus finch.

Throughout this chapter we have examined how ecologists use their understanding of populations to develop mathematical models that mimic natural patterns of population growth. Although populations commonly grow rapidly when at low densities, they become limited as the populations grow larger. The simplest population models are helpful starting points, but they are not sufficient for most species that have survival and fecundity rates that vary with age, size, or life history stage. Using life tables helps to incorporate this complexity. As we will see below in "Ecology Today: Connecting the Concepts," the analysis of life tables can be very helpful in setting priorities for management strategies to save species from extinction.

ECOLOGY TODAY CONNECTING THE CONCEPTS

SAVING THE SEA TURTLES

Sea turtles. Population models have identified the stages in life that need the most protection to allow turtle populations to recover. These models are relevant to all species of sea turtles, including this green sea turtle (*Chelonia mydas*) off the coast of Hawaii. Photo by Masa Ushioda/Image Quest Marine.

Under the cover of darkness, the swimmers come to shore. After spending a year out in the ocean, the female sea turtles crawl up the shore and dig a nest to lay their eggs. After about 2 months, these eggs will hatch and the hatchlings will scramble toward the ocean where they will face a gauntlet of predators. If they survive, they will need 2 or 3 decades to become reproductively mature. They may live for 80 years.

Not long ago, many more females came to shore. Of the six species of sea turtles, all have declined over the past several centuries. For example, scientists estimate that there were once 91 million green turtles (*Chelonia mydas*) in the Caribbean; today there are about 300 000 which is a decline of more than 99 percent. Sea turtles, which live in temperate and tropical waters, are declining worldwide. Historically, people hunted them for food

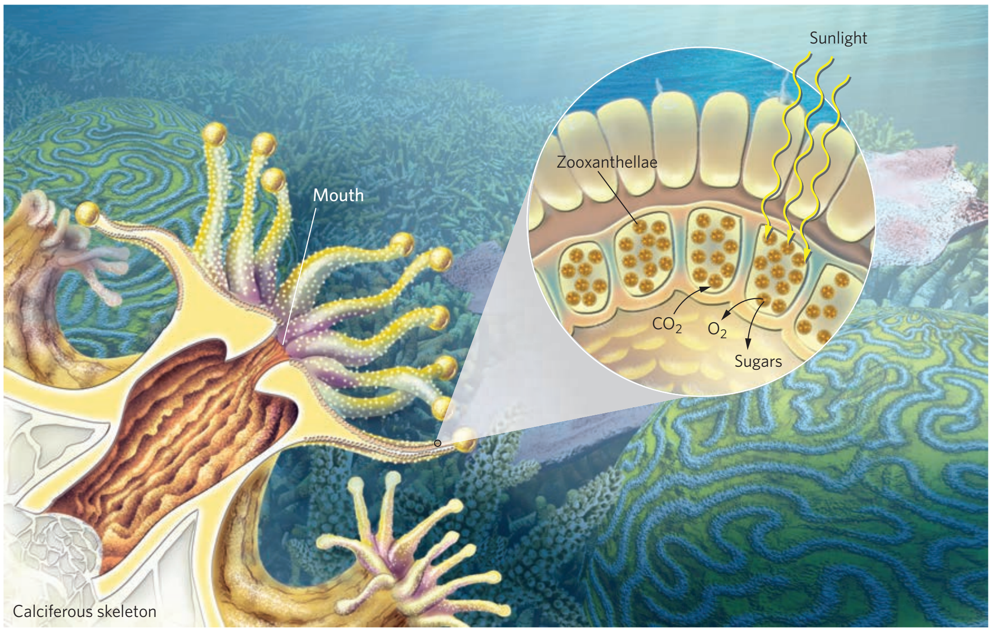


Figure 17.1 A mutualism between coral and zooxanthellae. A coral grabs food with its tentacles, which contain stinging cells, and pulls the food into its mouth. Zooxanthellae algae live along the surface of a coral's tentacles where they obtain sunlight for photosynthesis. Corals provide a place for algae to live and emit CO_2 that algae use in photosynthesis. As algae photosynthesize, they provide sugars and O_2 that corals consume.

Whale ancestor. The ancestor of modern whales, in the genus *Indohyus,* was a terrestrial animal that spent part of its time in the water. Over time, the descendants of this animal developed numerous adaptations for living in water that are found in modern-day whales.

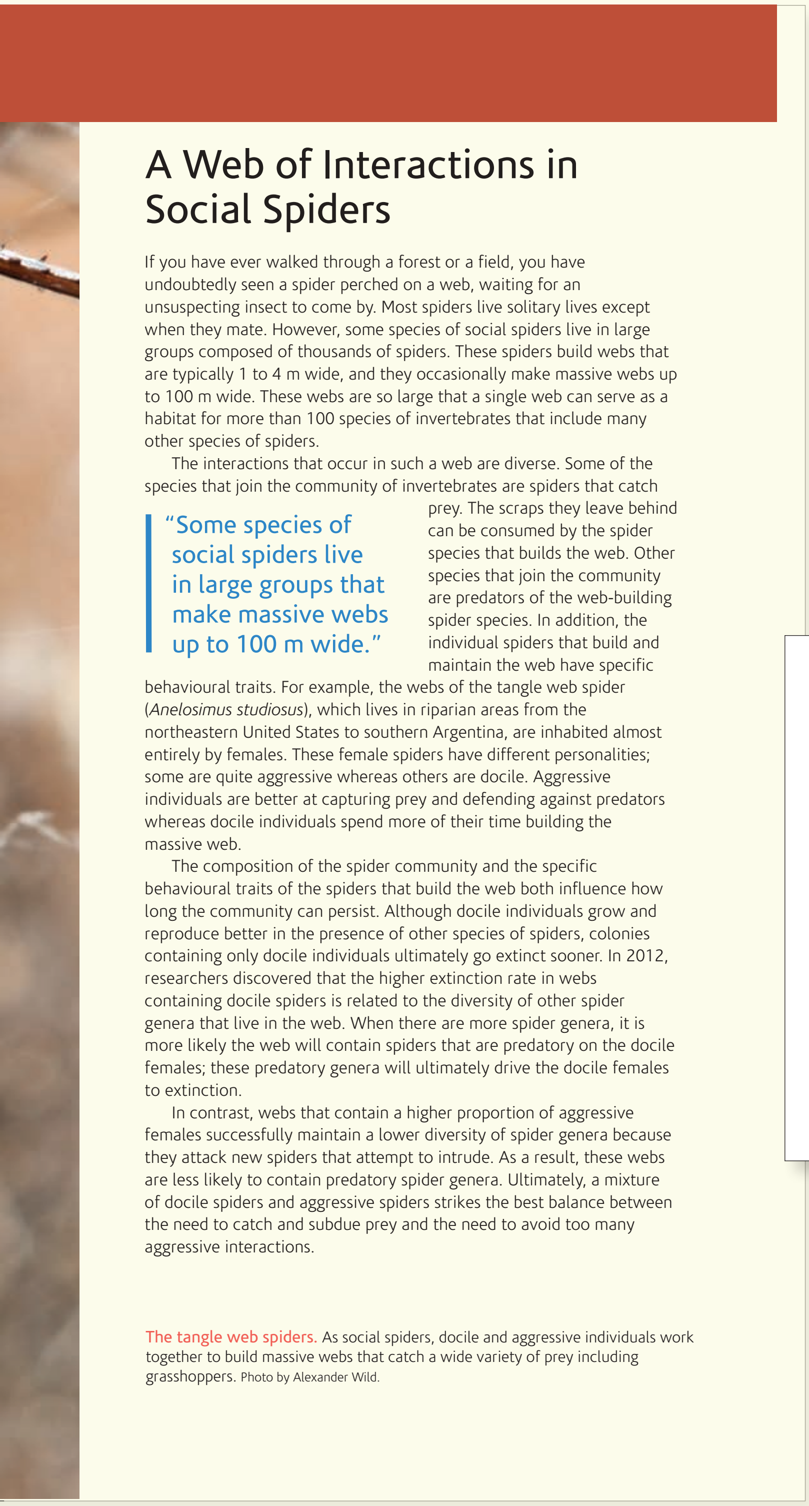
Figure 17.2 The green sea slug. When the slug first hatches from an egg, it is brown. However, as it begins to eat algae, it stores the chloroplasts from the algae in its own tissues. As the slug accumulates a large number of chloroplasts, its body turns green and it is able to acquire most of its energy through photosynthesis rather than through herbivory. Photo by Nicholas E. Curtis and Ray Martinez, University of South Florida.

Each chapter contains a wealth of contemporary and classic examples.

A modern approach to community and ecosystem ecology

CHAPTER 18

Community Structure



A Web of Interactions in Social Spiders

If you have ever walked through a forest or a field, you have undoubtedly seen a spider perched on a web, waiting for an unsuspecting insect to come by. Most spiders live solitary lives except when they mate. However, some species of social spiders live in large groups composed of thousands of spiders. These spiders build webs that are typically 1 to 4 m wide, and they occasionally make massive webs up to 100 m wide. These webs are so large that a single web can serve as a habitat for more than 100 species of invertebrates that include many other species of spiders.

The interactions that occur in such a web are diverse. Some of the species that join the community of invertebrates are spiders that catch prey. The scraps they leave behind can be consumed by the spider species that builds the web. Other species that join the community are predators of the web-building spider species. In addition, the individual spiders that build and maintain the web have specific behavioural traits. For example, the webs of the tangle web spider (*Anelosimus studiosus*), which lives in riparian areas from the northeastern United States to southern Argentina, are inhabited almost entirely by females. These female spiders have different personalities; some are quite aggressive whereas others are docile. Aggressive individuals are better at capturing prey and defending against predators whereas docile individuals spend more of their time building the massive web.

> "Some species of social spiders live in large groups that make massive webs up to 100 m wide."

The composition of the spider community and the specific behavioural traits of the spiders that build the web both influence how long the community can persist. Although docile individuals grow and reproduce better in the presence of other species of spiders, colonies containing only docile individuals ultimately go extinct sooner. In 2012, researchers discovered that the higher extinction rate in webs containing docile spiders is related to the diversity of other spider genera that live in the web. When there are more spider genera, it is more likely the web will contain spiders that are predatory on the docile females; these predatory genera will ultimately drive the docile females to extinction.

In contrast, webs that contain a higher proportion of aggressive females successfully maintain a lower diversity of spider genera because they attack new spiders that attempt to intrude. As a result, these webs are less likely to contain predatory spider genera. Ultimately, a mixture of docile spiders and aggressive spiders strikes the best balance between the need to catch and subdue prey and the need to avoid too many aggressive interactions.

The tangle web spiders. As social spiders, docile and aggressive individuals work together to build massive webs that catch a wide variety of prey including grasshoppers. Photo by Alexander Wild.

Enhanced coverage of species interactions, community ecology, and ecosystem ecology.

Figure 14.18 Chemical defences. The bombardier beetle (*Stenaptinus insignis*) mixes two chemicals inside its abdomen that react to release a boiling hot fluid to deter predators.

Highlights contemporary approaches and research throughout.

Integrated applications to medicine and public health

ECOLOGY TODAY CONNECTING THE CONCEPTS

DRUG-RESISTANT TUBERCULOSIS

Tuberculosis in Inuit communities. In Kangiqsualujjuaq, Quebec, more than 30 active cases of TB were reported in less than a year. Photo by Bryan and Cherry Alexander Photography/ ArcticPhoto/All Canada Photos.

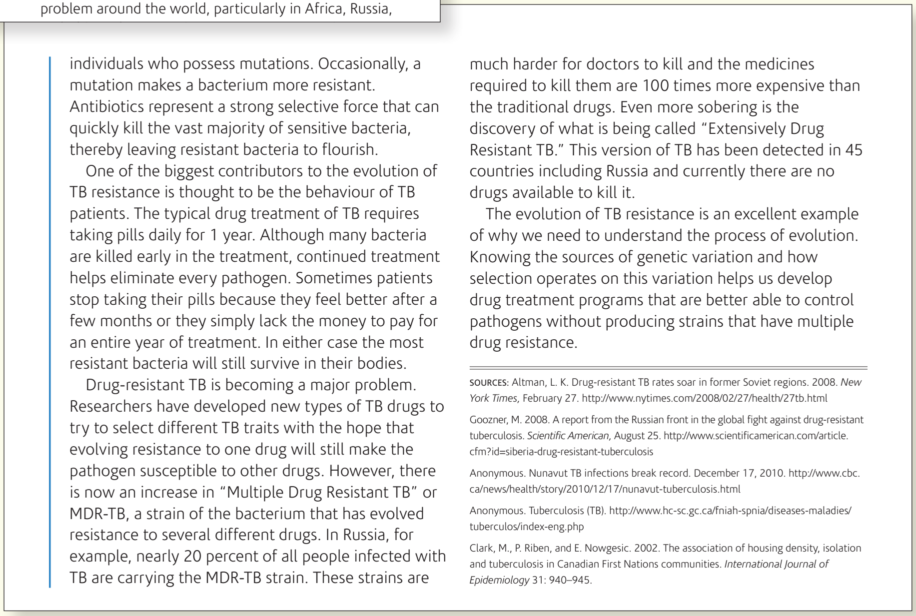
Tuberculosis, or TB, is a highly infectious disease caused by a bacterium (*Mycobacterium tuberculosis*). TB has killed people for thousands of years. In 2009, for example, researchers discovered that the preserved tissues of a woman who died 2600 years ago and was mummified have genetic markers of the TB bacterium. Today, experts estimate that nearly one-third of the world's human population is infected by the

extensive tissue damage, weakness, night sweats, and bloody sputum. It is highly contagious; when an infected individual coughs or talks, bacteria are expelled and can survive in the air for several hours and infect other people.

Around the world each year, 2 million people die of TB. Nationally, Canada has a rate of infection comparable to other industrialized nations. Canada-born, non-native groups show an incidence of 1 TB infection per 100 000 people. However, in Inuit communities, the rate is 155.8 per 100 000. In Nunavut, the rate of infection is 62 times higher than the national average. Northern communities are isolated and less likely to receive medical treatment and supplies to treat TB infections. Incomes in most Inuit communities are low, resulting in houses that are frequently in poor condition and lack insulation. The inability to properly heat these homes can make inhabitants more vulnerable to diseases. Many homes also lack proper ventilation, which increases the exposure to airborne bacteria, and most people live in cramped conditions, which can facilitate the spread of the bacterium. Despite efforts to improve these conditions and reduce the rate of infection, researchers estimate that the goal of reducing the rate to 1 per 100 000 Inuit may still be a long way off.

Drug-resistant tuberculosis is a rapidly growing problem around the world, particularly in Africa, Russia,

Numerous examples show the relevance of ecological concepts to contemporary issues in public health.



individuals who possess mutations. Occasionally, a mutation makes a bacterium more resistant. Antibiotics represent a strong selective force that can quickly kill the vast majority of sensitive bacteria, thereby leaving resistant bacteria to flourish.

One of the biggest contributors to the evolution of TB resistance is thought to be the behaviour of TB patients. The typical drug treatment of TB requires taking pills daily for 1 year. Although many bacteria are killed early in the treatment, continued treatment helps eliminate every pathogen. Sometimes patients stop taking their pills because they feel better after a few months or they simply lack the money to pay for an entire year of treatment. In either case the most resistant bacteria will still survive in their bodies.

Drug-resistant TB is becoming a major problem. Researchers have developed new types of TB drugs to try to select different TB traits with the hope that evolving resistance to one drug will still make the pathogen susceptible to other drugs. However, there is now an increase in "Multiple Drug Resistant TB" or MDR-TB, a strain of the bacterium that has evolved resistance to several different drugs. In Russia, for example, nearly 20 percent of all people infected with TB are carrying the MDR-TB strain. These strains are much harder for doctors to kill and the medicines required to kill them are 100 times more expensive than the traditional drugs. Even more sobering is the discovery of what is being called "Extensively Drug Resistant TB." This version of TB has been detected in 45 countries including Russia and currently there are no drugs available to kill it.

The evolution of TB resistance is an excellent example of why we need to understand the process of evolution. Knowing the sources of genetic variation and how selection operates on this variation helps us develop drug treatment programs that are better able to control pathogens without producing strains that have multiple drug resistance.

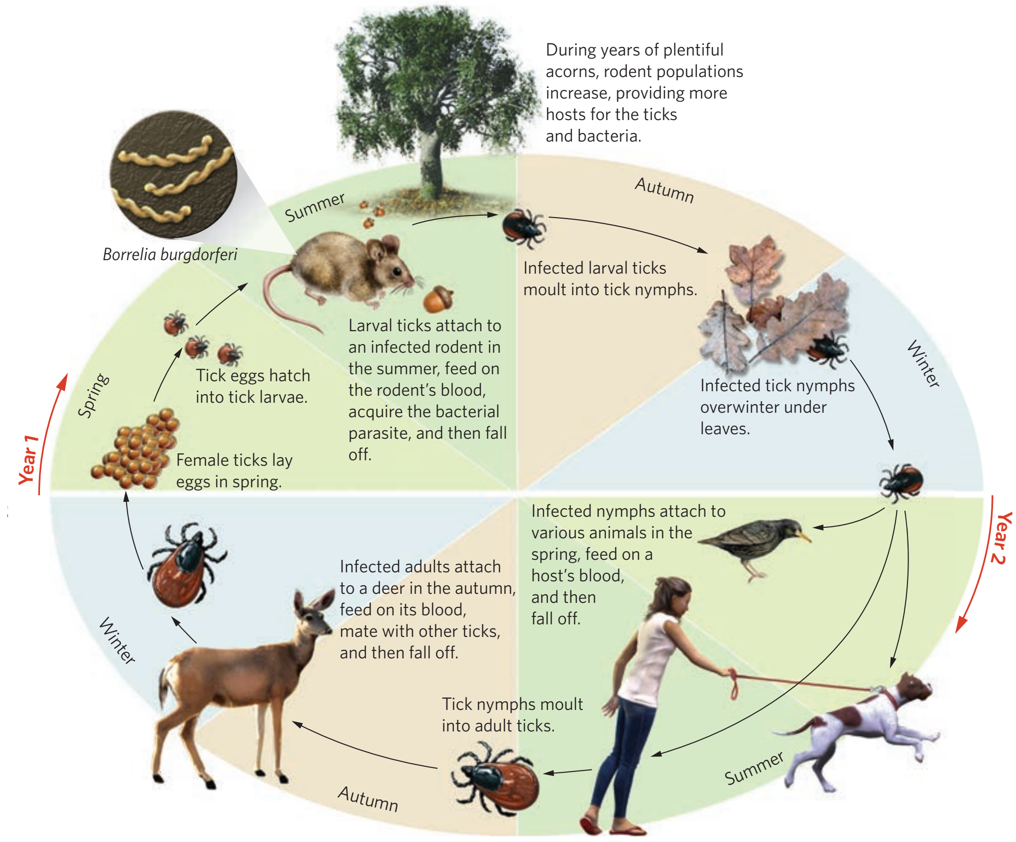
SOURCES: Altman, L. K. Drug-resistant TB rates soar in former Soviet regions. 2008. *New York Times*, February 27. http://www.nytimes.com/2008/02/27/health/27tb.html

Goozner, M. 2008. A report from the Russian front in the global fight against drug-resistant tuberculosis. *Scientific American*, August 25. http://www.scientificamerican.com/article.cfm?id=siberia-drug-resistant-tuberculosis

Anonymous. Nunavut TB infections break record. December 17, 2010. http://www.cbc.ca/news/health/story/2010/12/17/nunavut-tuberculosis.html

Anonymous. Tuberculosis (TB). http://www.hc-sc.gc.ca/fniah-spnia/diseases-maladies/tuberculos/index-eng.php

Clark, M., P. Riben, and E. Nowgesic. 2002. The association of housing density, isolation and tuberculosis in Canadian First Nations communities. *International Journal of Epidemiology* 31: 940–945.



The cycle of Lyme disease. A diverse array of species affects the prevalence of the bacterium that causes Lyme disease. The cycle begins when ticks attach themselves to infected rodents and become infected with the bacterium. After they drop from the rodents, they moult into nymphs and spend the winter under leaves. In the spring the nymphs attach themselves to hosts again and then drop and moult into adults. As adults, most ticks attach themselves to deer, search for mates, and then lay eggs. During years of high acorn production by oak trees, there is an abundance of food for rodents that produces large rodent populations. Large rodent populations lead to large tick populations that can infect a variety of animals including deer and humans.

Students see how ecological thinking is essential to our understanding of infectious disease.

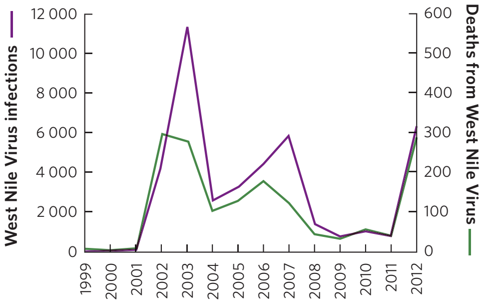
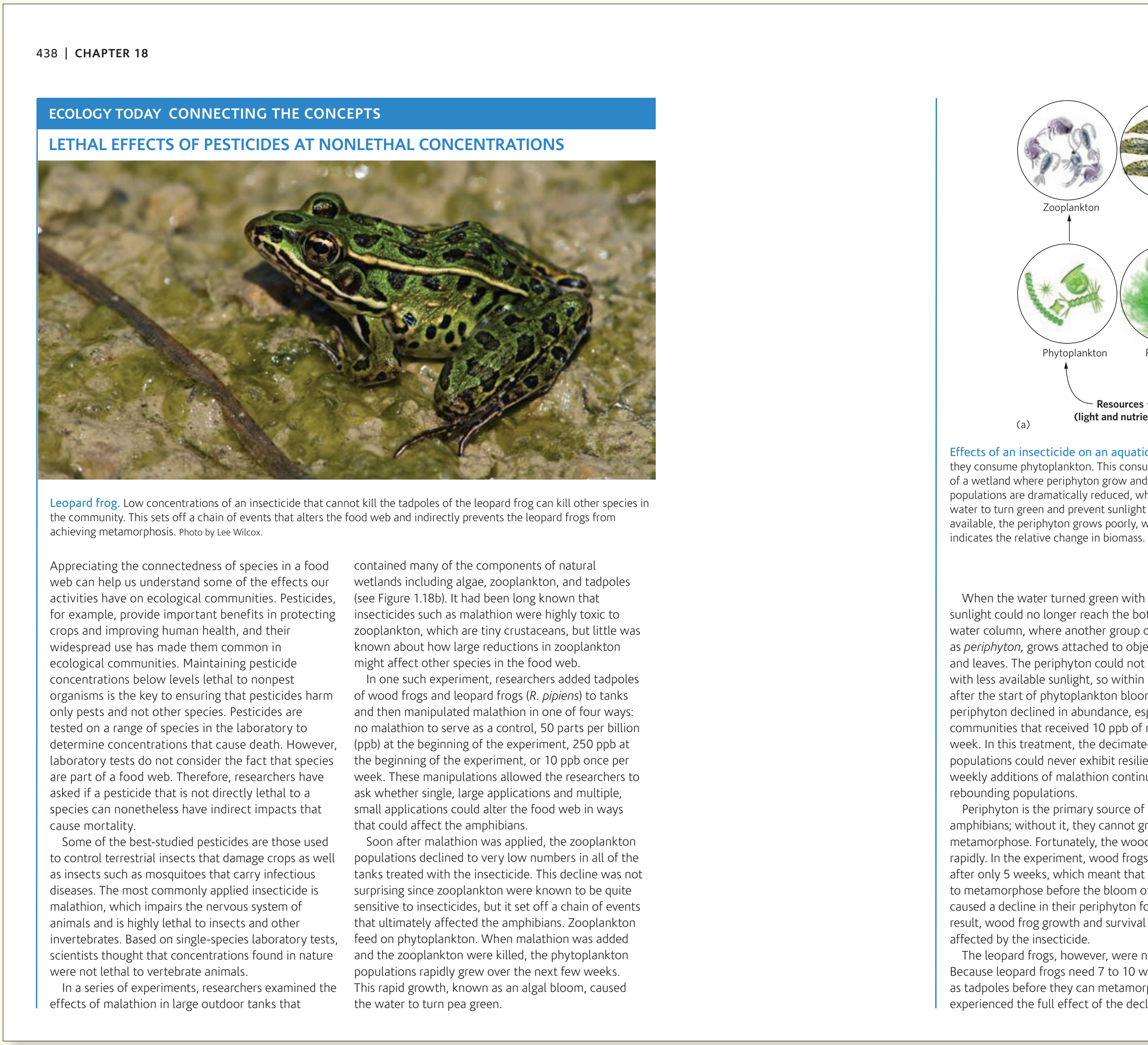


Figure 15.4 Human infections and deaths from West Nile virus in Canada and the United States. Following the introduction of the virus to North America in 1999, the number of human infections and deaths rose rapidly through 2003. Efforts to control mosquito populations, which carry the virus, caused a sharp decline in these effects on humans through 2011. In 2012, however, unusually warm temperatures with high precipitation in some regions resulted in large mosquito populations and a new surge in West Nile infections and deaths. Note that the two *y* axes have different scales. Data from http://www.cdc.gov/ncidod/dvbid/westnile/surv&control.htm#maps.

Fosters ecological literacy through applications to conservation and the environment



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ECOLOGY TODAY CONNECTING THE CONCEPTS

LETHAL EFFECTS OF PESTICIDES AT NONLETHAL CONCENTRATIONS

Leopard frog. Low concentrations of an insecticide that cannot kill the tadpoles of the leopard frog can kill other species in the community. This sets off a chain of events that alters the food web and indirectly prevents the leopard frogs from achieving metamorphosis. Photo by Lee Wilcox.

Appreciating the connectedness of species in a food web can help us understand some of the effects our activities have on ecological communities. Pesticides, for example, provide important benefits in protecting crops and improving human health, and their widespread use has made them common in ecological communities. Maintaining pesticide concentrations below levels lethal to nonpest organisms is the key to ensuring that pesticides harm only pests and not other species. Pesticides are tested on a range of species in the laboratory to determine concentrations that cause death. However, laboratory tests do not consider the fact that species are part of a food web. Therefore, researchers have asked if a pesticide that is not directly lethal to a species can nonetheless have indirect impacts that cause mortality.

Some of the best-studied pesticides are those used to control terrestrial insects that damage crops as well as insects such as mosquitoes that carry infectious diseases. The most commonly applied insecticide is malathion, which impairs the nervous system of animals and is highly lethal to insects and other invertebrates. Based on single-species laboratory tests, scientists thought that concentrations found in nature were not lethal to vertebrate animals.

In a series of experiments, researchers examined the effects of malathion in large outdoor tanks that contained many of the components of natural wetlands including algae, zooplankton, and tadpoles (see Figure 1.18b). It had been long known that insecticides such as malathion were highly toxic to zooplankton, which are tiny crustaceans, but little was known about how large reductions in zooplankton might affect other species in the food web.

In one such experiment, researchers added tadpoles of wood frogs and leopard frogs (*R. pipiens*) to tanks and then manipulated malathion in one of four ways: no malathion to serve as a control, 50 parts per billion (ppb) at the beginning of the experiment, 250 ppb at the beginning of the experiment, or 10 ppb once per week. These manipulations allowed the researchers to ask whether single, large applications and multiple, small applications could alter the food web in ways that could affect the amphibians.

Soon after malathion was applied, the zooplankton populations declined to very low numbers in all of the tanks treated with the insecticide. This decline was not surprising since zooplankton were known to be quite sensitive to insecticides, but it set off a chain of events that ultimately affected the amphibians. Zooplankton feed on phytoplankton. When malathion was added and the zooplankton were killed, the phytoplankton populations rapidly grew over the next few weeks. This rapid growth, known as an algal bloom, caused the water to turn pea green.

Effects of an insecticide on an aquatic
they consume phytoplankton. This consu
of a wetland where periphyton grow and
populations are dramatically reduced, wh
water to turn green and prevent sunlight
available, the periphyton grows poorly, w
indicates the relative change in biomass.

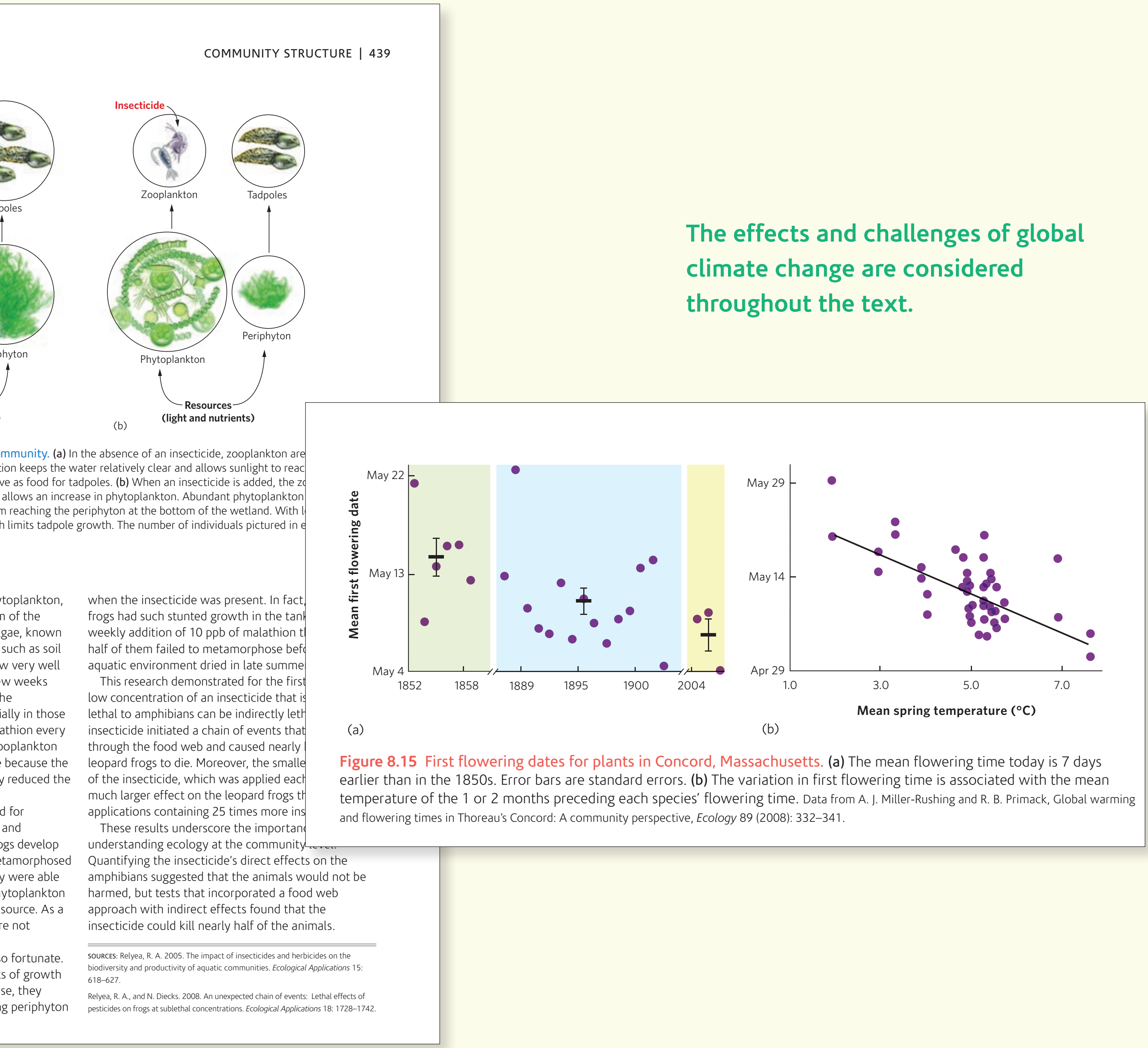
When the water turned green with
sunlight could no longer reach the bo
water column, where another group c
as *periphyton,* grows attached to obje
and leaves. The periphyton could not
with less available sunlight, so within
after the start of phytoplankton bloo
periphyton declined in abundance, es
communities that received 10 ppb of
week. In this treatment, the decimate
populations could never exhibit resilie
weekly additions of malathion contin
rebounding populations.

Periphyton is the primary source of
amphibians; without it, they cannot g
metamorphose. Fortunately, the woo
rapidly. In the experiment, wood frogs
after only 5 weeks, which meant that
to metamorphose before the bloom o
caused a decline in their periphyton f
result, wood frog growth and survival
affected by the insecticide.

The leopard frogs, however, were n
Because leopard frogs need 7 to 10 w
as tadpoles before they can metamor
experienced the full effect of the dec

Each chapter closes with ECOLOGY TODAY: CONNECTING THE CONCEPTS, a case study that applies multiple chapter concepts to a contemporary ecological issue.

The effects and challenges of global climate change are considered throughout the text.



mmunity. **(a)** In the absence of an insecticide, zooplankton are
tion keeps the water relatively clear and allows sunlight to reac
ve as food for tadpoles. **(b)** When an insecticide is added, the zo
allows an increase in phytoplankton. Abundant phytoplankton
m reaching the periphyton at the bottom of the wetland. With l
h limits tadpole growth. The number of individuals pictured in e

ytoplankton,
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when the insecticide was present. In fact,
frogs had such stunted growth in the tank
weekly addition of 10 ppb of malathion t
half of them failed to metamorphose bef
aquatic environment dried in late summe

This research demonstrated for the first
low concentration of an insecticide that i
lethal to amphibians can be indirectly leth
insecticide initiated a chain of events that
through the food web and caused nearly
leopard frogs to die. Moreover, the smalle
of the insecticide, which was applied each
much larger effect on the leopard frogs th
applications containing 25 times more ins

These results underscore the importan
understanding ecology at the community
Quantifying the insecticide's direct effects on the amphibians suggested that the animals would not be harmed, but tests that incorporated a food web approach with indirect effects found that the insecticide could kill nearly half of the animals.

SOURCES: Relyea, R. A. 2005. The impact of insecticides and herbicides on the biodiversity and productivity of aquatic communities. *Ecological Applications* 15: 618–627.

Relyea, R. A., and N. Diecks. 2008. An unexpected chain of events: Lethal effects of pesticides on frogs at sublethal concentrations. *Ecological Applications* 18: 1728–1742.

Figure 8.15 First flowering dates for plants in Concord, Massachusetts. **(a)** The mean flowering time today is 7 days earlier than in the 1850s. Error bars are standard errors. **(b)** The variation in first flowering time is associated with the mean temperature of the 1 or 2 months preceding each species' flowering time. Data from A. J. Miller-Rushing and R. B. Primack, Global warming and flowering times in Thoreau's Concord: A community perspective, *Ecology* 89 (2008): 332–341.

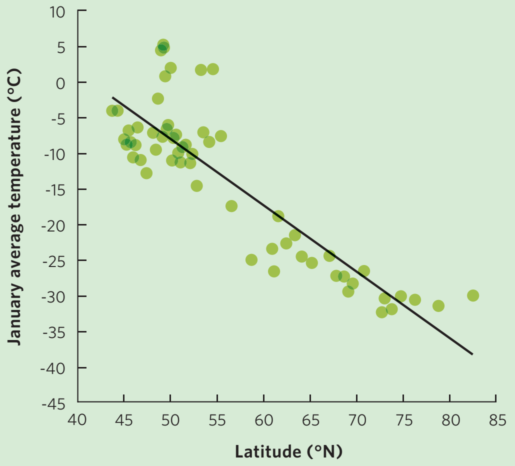
A learning-by-doing approach to basic quantitative tools and the use of data

ANALYZING ECOLOGY

Regressions

As we have discussed, latitudes closer to the equator receive more solar radiation than latitudes closer to the poles. Given this observation, lower latitudes should also have warmer temperatures than higher latitudes. In fact, understanding the nature of this relationship would help us determine exactly how much temperature changes with latitude. When we want to know how one variable changes in relation to another, we use a statistical tool called **regression.** In Chapter 4 we saw that a correlation determines if there is a relationship between two variables. A regression determines whether there is a relationship and also describes the nature of that relationship.

To help illustrate this idea, we can use data on the average January temperature from 59 locations spanning Canada from north to south. If we plot the relationship between location latitude and average location temperature in January, we obtain the following graph:



In this case, the relationship between the two variables follows a straight line; we have drawn a line of best fit through the distribution of the data points. This is a regression line because it represents the relationship between the two variables. It informs us about the nature of the relationship through the slope and intercept of the line. For these data, the regression can be described using the equation of a straight line, where Y is the dependent variable, X is the independent variable, m is the slope of the line, and b is the Y-intercept of the line at the point where $X = 0$. In this example, the slope is -0.9 and the intercept is 38:

$$Y = mX + b$$

$$\text{Temperature} = -0.9 \times \text{Latitude} + 39$$

This regression equation tells us that for every 1 degree increase in latitude, the average temperature in January decreases by 0.9°C. Note that while the simplest form of a regression is a straight line, regression lines can also be curvilinear.

YOUR TURN Based on the relationship between latitude and temperature, use the regression equation to estimate the average January temperature at 40, 60, and 80 degrees of latitude.

Regression A statistical tool that determines whether there is a relationship between two variables and that also describes the nature of that relationship.

ANALYZING ECOLOGY introduces mathematical and statistical techniques in relevant research contexts. YOUR TURN self-guided study problems provide opportunities for practice.

PRACTICING ECOLOGY problems help students to gain experience graphing and interpreting real data.

PRACTICING ECOLOGY: THE COST OF HAVING A BODYGUARD

Jacques Brodeur from Université de Montréal and his colleagues study interactions between herbivores and their enemies. Photo by Anne Audy.

As we have seen in this chapter, many parasites complete part of their life cycle by manipulating the body of a host. However, in order to control its host, a parasite must expend energy. Often, a host ceases to feed once infected, so the energy that the parasite uses must come from stored energy that the parasite could otherwise use for its own development. In addition, the body manipulation necessarily requires that the parasite transfer chemical compounds to the host's brain, and these chemicals are likely expensive to produce. Do these costs detract from the fitness of the parasite?

Dinocampus coccinellae is a parasitic wasp that lays a single egg inside the spotted lady beetle (*Coleomegilla maculata*). After feeding on the beetle's eggs, gonads, and fat reserves, the larva paralyzes the beetle and emerges from the anal gland as a pupa. The pupa then spins a cocoon around the legs of the beetle and develops for an average of 7 days until it emerges as an adult wasp. Only 25 percent of beetles survive during the time that the pupa is in its cocoon. A beetle that does survive exhibits bodyguard behaviour over the cocoon; the pupa makes the beetle twitch when provoked by an external stimulus and this behaviour reduces predation on the pupa. However, the pupa must use energy to control the beetle's behaviour. We might hypothesize that this energy expense comes at a cost to the future fitness of the parasitic wasp.

Jacques Brodeur from the Université de Montréal and his colleagues tested this hypothesis by observing parasitized beetles in the laboratory. They collected wasps and beetles from the field and allowed the wasps to parasitize the beetles in the lab. After pupae emerged from the beetles and spun cocoons, the researchers recorded the number of days each beetle exhibited twitching behaviour, which corresponds to the amount of time the beetle survived and the pupa was able to control its movement. Once the wasps emerged from their cocoons, the researchers counted the number of eggs in female wasps as a measure of wasp fitness. You can view their data in the table.

DURATION OF BEETLE TWITCHING BEHAVIOUR (DAYS) AND NUMBER OF EGGS IN EMERGENT FEMALE WASPS

DURATION OF TWITCHING BEHAVIOUR	NUMBER OF EGGS
2.9	103
4.9	102
4	102
7.9	101
8.9	99
9	98
7	100
5.9	100
6.1	101
7	103
4.9	101
8	99

GRAPH THE DATA

1. Create a scatterplot graph with duration of twitching behaviour on the *x* axis and number of eggs in emergent wasps on the *y* axis.

2. Visually estimate and draw a regression line of best fit through the data.

INTERPRET THE DATA

1. Explain how the data support or refute the hypothesis that the energy expense of controlling a lady beetle host comes at a cost to future fitness of the developing wasp.

2. Unlike animals that are born with a fixed number of eggs, female *D. coccinellae* wasps are able to produce eggs throughout their lifetime. How might the later production of eggs compensate for the fitness cost of controlling the behaviour of a host beetle?

3. In the same study, the researchers found no relationship between duration of beetle twitching behaviour and the emergent wasp's lifespan. However, the amount of food after emergence positively correlated with wasp lifespan. What does this suggest about the allocation of energy for fecundity versus energy allocated to survival in *D. coccinellae*?

SOURCE: Maure, F., J. Brodeur, N. Ponlet, J. Doyon, A. Firlej, E. Elguero, and F. Thomas. 2011. The cost of a bodyguard. *Biology Letters*, 7: 843–846.

Over 500 graphs throughout the text present and describe actual research data.

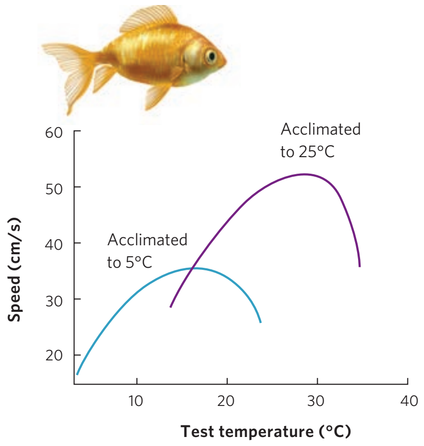


Figure 4.9 Acclimation to different temperatures. Goldfish raised at low temperatures swim faster in cold water and more slowly in warmer water. Individuals raised at high temperatures swim faster in warmer water than in cold water. After F. E. J. Fry and J. S. Hart, Cruising speed of goldfish in relation to water temperature, *J. Fish. Res. Bd. Can.* 7 (1948): 169–174.

Focus on scientific method and the process of discovery

CHAPTER 19

Community Succession

The rate of glacier retreat. Historic observations by Captain George Vancouver, John Muir, William Cooper, and current researchers indicate that the glacier at Glacier Bay has retreated rapidly during the past 200 years.

responded to the massive disturbance of an advancing and retreating glacier.

The observations of Vancouver, Muir, and Cooper paved the way for more than a century of subsequent ecological research at Glacier Bay. In fact, the original terrestrial quadrats set up by Cooper are still monitored today, as are local streams that have been created by the melting glacier. As we will see in this chapter, long-term changes in ecological communities follow predictable patterns, which are important for us to understand the ways in which terrestrial and aquatic communities change over time and the processes that underlie these changes.

SOURCES: W. S. Cooper, The recent ecological history of Glacier Bay, Alaska II: The present vegetation cycle, *Ecology* 4 (1923): 223–246.

C. L. Fastie, Causes and ecosystem consequences of multiple pathways of primary succession at Glacier Bay, Alaska, *Ecology* 76 (1995): 1899–1916.

Students learn how researchers formulate and test their hypotheses. The text shows how researchers challenge and extend the work of those who came before them.

Retreating Glaciers in Alaska

In the panhandle of Alaska near Juneau, a stretch of land has undergone incredible changes during the past 200 years. In 1794, Captain George Vancouver found an inlet that headed toward modern-day Juneau. To the north of the inlet was a massive glacier that measured more than 1 km thick and 32 km wide. When the naturalist John Muir visited the glacier site in 1879, 85 years after Captain Vancouver's expedition, he was shocked to find that the glacier had receded nearly 80 km and left behind a large bay. Moreover, while most bays in Alaska were heavily forested, the shores of this new bay were relatively barren. As Muir explored, he found several locations with large stumps that were the remnants of hemlock, black cottonwood (*Populus trichocarpa*), and Sitka spruce trees that had been sheared off by the glacier as it advanced centuries earlier. Muir had no way of knowing that h
was looking at one of the
fastest melting glaciers in
the world.

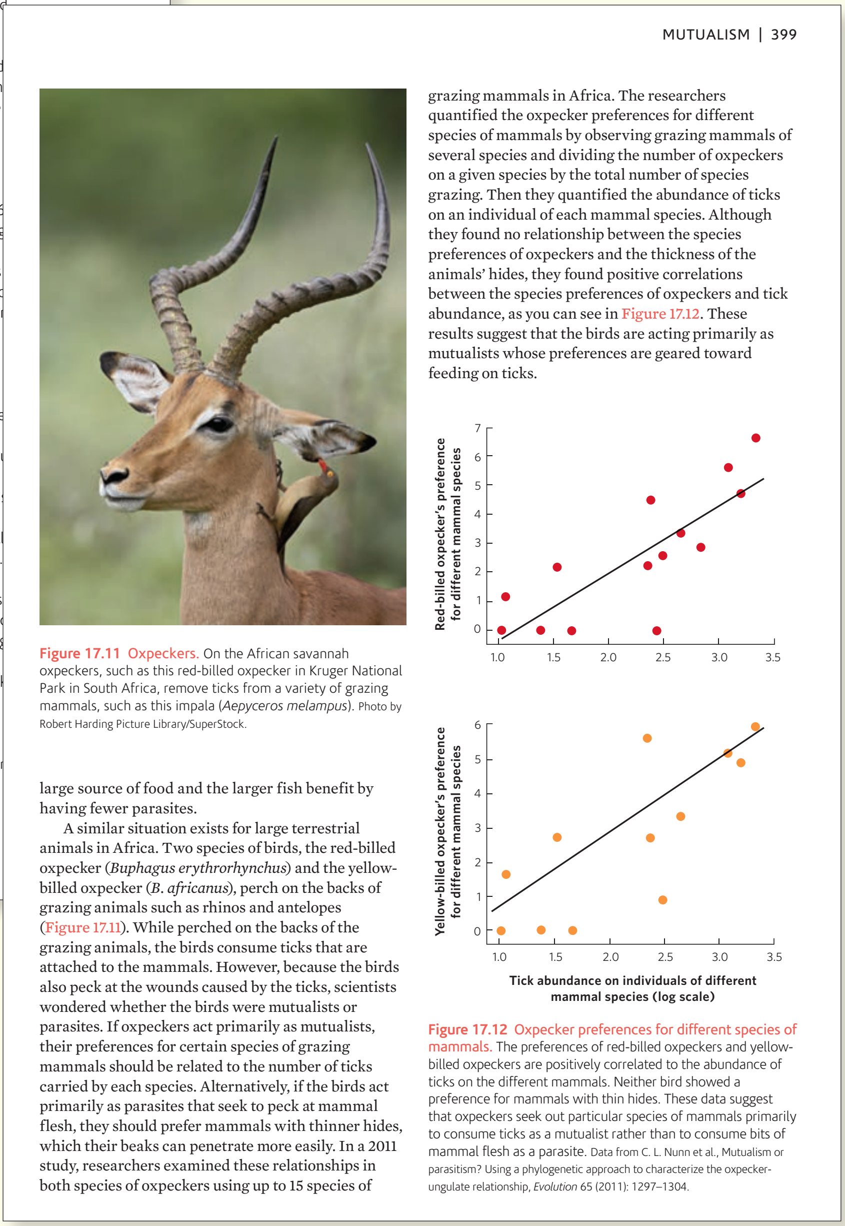
> "When the naturalist John Muir visited the glacier site in 1879, 85 years after Captain Vancouver's expedition, he was shocked to find that the glacier had receded nearly 80 km and left behind a large bay."

John Muir's writings about the natural world were widely read. In 1916
William Cooper, an ecolog
who was particularly
intrigued by Muir's stories
Alaska, made the first of several expeditions to the site that came t
be known as Glacier Bay. On these expeditions, he surveyed the pla
growing at various sites along the shore of the bay, including sites where the glacier existed during Vancouver's visit, sites where the glacier existed during Muir's visit, and sites where the glacier had receded only recently. He also set up quadrats around the bay to record the changes in vegetation at various locations that he planne
to check when he returned on subsequent expeditions.

Cooper reasoned that sites exposed for the longest duration wou
have the most time to grow back into the kind of forest that had existed before the glaciers had advanced centuries earlier. In contras
he expected recently exposed sites to be bare rock and gravel, representing the first stages of a developing forest. On these recentl
exposed sites, Cooper found mosses, lichens, herbs, and low shrubs. Sites that had been exposed for 35 to 45 years had tall species of willow and alder shrubs (*Alnus sinuata*) and black cottonwood trees
Sites older than 100 years contained Sitka spruce trees, and sites ol
than 160 years had hemlock in the understorey. By examining chang
in the plant community at sites that had been exposed for different lengths of time, he was able to hypothesize how the forests of Alask

Glacier Bay, Alaska. In 1794, a glacier that was more than 1200 m thick covered all but the inlet of the bay. Since then, the glaciers have melted a
retreated, leaving behind a large body of water. Photo by Ron Niebrugge/wildnatureimages.com.

Chapters present research from across the globe.



MUTUALISM | 399

Figure 17.11 Oxpeckers. On the African savannah oxpeckers, such as this red-billed oxpecker in Kruger National Park in South Africa, remove ticks from a variety of grazing mammals, such as this impala (*Aepyceros melampus*). Photo by Robert Harding Picture Library/SuperStock.

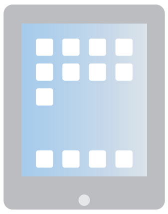
large source of food and the larger fish benefit by having fewer parasites.

A similar situation exists for large terrestrial animals in Africa. Two species of birds, the red-billed oxpecker (*Buphagus erythrorhynchus*) and the yellow-billed oxpecker (*B. africanus*), perch on the backs of grazing animals such as rhinos and antelopes (Figure 17.11). While perched on the backs of the grazing animals, the birds consume ticks that are attached to the mammals. However, because the birds also peck at the wounds caused by the ticks, scientists wondered whether the birds were mutualists or parasites. If oxpeckers act primarily as mutualists, their preferences for certain species of grazing mammals should be related to the number of ticks carried by each species. Alternatively, if the birds act primarily as parasites that seek to peck at mammal flesh, they should prefer mammals with thinner hides, which their beaks can penetrate more easily. In a 2011 study, researchers examined these relationships in both species of oxpeckers using up to 15 species of grazing mammals in Africa. The researchers quantified the oxpecker preferences for different species of mammals by observing grazing mammals of several species and dividing the number of oxpeckers on a given species by the total number of species grazing. Then they quantified the abundance of ticks on an individual of each mammal species. Although they found no relationship between the species preferences of oxpeckers and the thickness of the animals' hides, they found positive correlations between the species preferences of oxpeckers and tick abundance, as you can see in Figure 17.12. These results suggest that the birds are acting primarily as mutualists whose preferences are geared toward feeding on ticks.

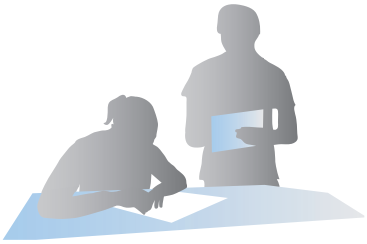
Figure 17.12 Oxpecker preferences for different species of mammals. The preferences of red-billed oxpeckers and yellow-billed oxpeckers are positively correlated to the abundance of ticks on the different mammals. Neither bird showed a preference for mammals with thin hides. These data suggest that oxpeckers seek out particular species of mammals primarily to consume ticks as a mutualist rather than to consume bits of mammal flesh as a parasite. Data from C. L. Nunn et al., Mutualism or parasitism? Using a phylogenetic approach to characterize the oxpecker-ungulate relationship, *Evolution* 65 (2011): 1297–1304.

Resources for Instructors and Students Create an Enhanced Teaching and Learning Experience

Test bank More than 1400 questions test student understanding and integration of the concepts at six different levels from knowledge and comprehension checks to application, analysis, synthesis, and evaluation.

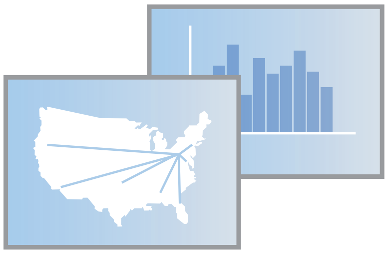


e-Book A complete online version of the textbook that allows the reader to highlight, bookmark, and add notes.



Activities Classroom activities use proven active learning techniques to engage students with the material and to encourage critical thinking.

Pre-lecture quizzes Quizzes for each concept heading help ensure that students have read the material before attending class.



Enhanced lectures for PowerPoint presentations Lecture slides using dynamic, layered art taken directly from the text

Optimized art Photos and illustrations from the text in both JPEG and PowerPoint formats.

LaunchPad An intuitive on-line homework, e-Book, and class-management system that provides curated resources compiled into ready-to-use teaching units, complete with problem sets, activities, e-book sections, and state-of-the-art online quizzing and testing.

Flash cards Key terms and definitions in interactive flashcards.

LearningCurve A set of assessment activities that uses a game-like interface to guide students through a series of questions tailored to individual understanding. Personalized study plans are generated based on quiz results.

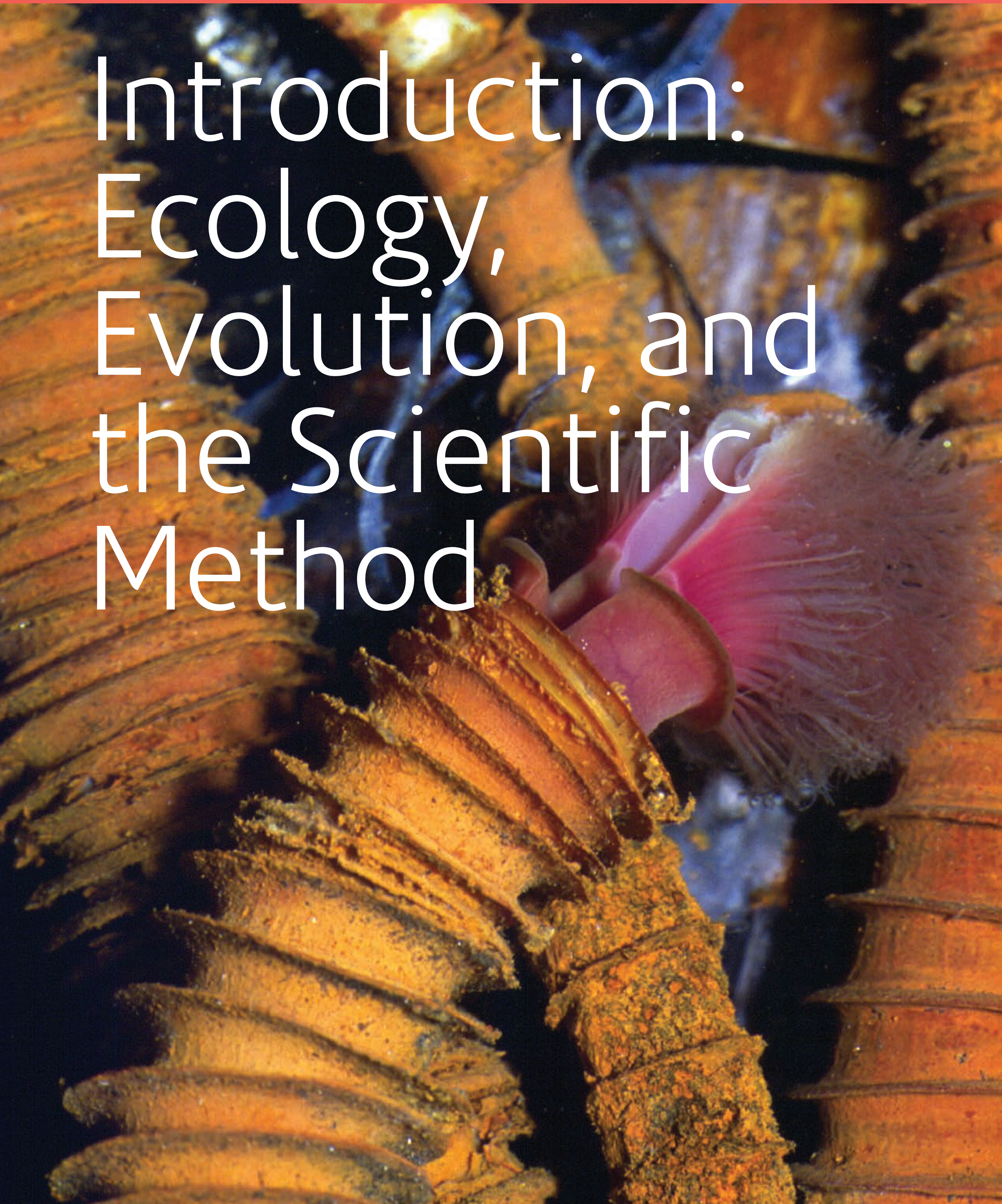
Canadian Edition

Ecology

The Economy of Nature

CHAPTER 1

Introduction: Ecology, Evolution, and the Scientific Method



Searching for Life at the Bottom of the Ocean

In the early 1800s, scientists hypothesized that deep ocean waters were devoid of life. Although unable to explore the deepest regions of the ocean at that time, they knew that sunlight could not penetrate depths greater than 275 m. Without sunlight there can be no photosynthesis, and without photosynthesis there can be no plants or algae to serve as food for other organisms. The cold temperatures and extreme pressures of deep ocean waters were also thought to contribute to the absence of deep-sea life. Given that ocean depths can exceed 10 000 m, it was reasonable to hypothesize that the deepest areas of the ocean could not support life.

As exploration continued throughout the nineteenth century, scientists began to collect organisms from ever greater ocean depths and their ideas about the limits of life began to change. In an 1873 expedition, scientists aboard the British research ship HMS *Challenger* dragged a large, open-sided, heavy box that was suspended from long ropes behind the ship across the floor of the Atlantic Ocean. This box—known as a dredge—sampled the sea floor in different parts of the ocean at depths of up to 4572 m. The scientists were astonished to discover nearly 5000 previously unknown species. When it became clear that life flourished at depths beyond the penetration of light, scientists were forced to reject their earlier hypothesis that no life existed in the deep ocean waters.

> "How could so much life exist at the bottom of the ocean?"

After discovering this rich abundance of deep-sea life, scientists were faced with the need to understand how it could exist. The lack of light suggested that deep-sea organisms were somehow sustained by energy that did not come from photosynthesis on the ocean floor. Scientists had observed that the surface waters of the ocean produced a steady descent of tiny particles that were produced by the death and decomposition of organisms living in the surface waters of the ocean. These particles are known as "marine snow." In addition to marine snow, large organisms, such as whales, occasionally died and fell to the ocean floor. Scientists hypothesized that marine snow and the remains of large organisms such as whales provided the energy needed to sustain organisms in the depths of the ocean.

In the 1970s, scientists were finally able to send submersibles—small manned submarines—to take a first-hand look at the deepest ocean areas. Their discoveries were shocking. They not only confirmed that much of the ocean floor supported living organisms, but that areas near openings in the floor of the ocean, which later came to be known as *hydrothermal vents,* contained a great diversity of deep-sea species. Hydrothermal vents release plumes of hot water with high concentrations of sulphur compounds and other mineral nutrients. A tremendous diversity of species surrounded these hydrothermal vents, including tubeworms, clams, crabs, and fish. Indeed, the total amount of life at these depths rivaled that seen in some of the most diverse places on Earth. It became clear that the amount of energy contained

A deep-sea vent. In some regions of the ocean floor, hot water containing sulphur compounds is released from the ground. The sulphur compounds provide energy for chemosynthetic bacteria, which then serve as food for many other species that live near the vents, including these rust-coloured tube worms (*Tevnia jerichonana*) that have been stained orange by iron compounds emitted from the vents. Photo by Peter Batson/Image Quest Marine.

in the descending organic matter—the marine snow—was not sufficient to support such a diverse and abundant set of life forms. That earlier hypothesis now had to be rejected.

How could so much life exist at the bottom of the ocean? That this life existed near the hydrothermal vents suggested that the vents were somehow responsible. Scientists had known for a long time that some species of bacteria could obtain their energy from chemicals rather than from the Sun. The bacteria use the energy in chemical bonds, combined with carbon dioxide (CO_2), to produce organic compounds—a process known as *chemosynthesis*—similar to the way that plants and algae use the energy of the Sun and CO_2 to produce organic compounds through photosynthesis. Based on this knowledge, scientists hypothesized that the hot vents, which release water with dissolved hydrogen sulphide gas and other chemicals, provided a source of energy for bacteria and that these bacteria could be consumed by the other organisms living around the vents. After several years of investigations, scientists found that the immediate area around the hot vents contained a group of organisms known as tubeworms, which can grow to more than 2 m long. These animals have no digestive system, but possess specialized organs that house vast numbers of chemosynthetic bacteria that live in a symbiotic relationship with the tubeworms. The tubeworms capture the sulphide gases and CO_2 from the surrounding water and pass these compounds to the bacteria, which then use the sulphide gases and CO_2 to produce organic compounds. Some of these organic compounds are passed to the tubeworms, which use them as food. These bacteria also represent a food source for many of the other animals that live near the vents. In turn, these bacteria-consuming animals can be consumed by larger animals, such as fish.

The story of the deep-sea vents reveals how scientists work: They make observations, devise hypotheses, test the hypotheses to confirm or reject them, and, if a hypothesis is rejected, devise a new hypothesis. As you will see throughout this chapter and subsequent chapters, science is an ongoing process that often leads to fascinating discoveries about how nature works.

SOURCES: Dubilier, et al., Symbiotic diversity in marine animals: The art of harnessing chemosynthesis, *Nature Reviews Microbiology* 6 (2008): 725–740.

R. R. Dunn. *Every Living Thing* (Harper Collins, 2002).

CHAPTER CONCEPTS

- Ecological systems exist in a hierarchical organization.
- Ecological systems are governed by physical and biological principles.
- Different organisms play diverse roles in ecological systems.
- Scientists use several approaches to studying ecology.
- Humans influence ecological systems.

The story of deep-sea vents offers an excellent introduction to the science of ecology. **Ecology** is the scientific study of the abundance and distribution of organisms in relation to other organisms and environmental conditions. The word ecology is taken from the Greek oikos, meaning "house," and thus refers to our immediate surroundings, or environment.

Although Charles Darwin never used the word *ecology* in his writings, he appreciated the importance of beneficial and harmful interactions among species. In his book, *On the Origin of Species*, published in 1859, Darwin compared the large number of interactions among species in nature to the large number of interactions among consumers and businesses in human economic systems. He

Ecology The scientific study of the abundance and distribution of organisms in relation to other organisms and environmental conditions.

described species interactions as "the economy of nature."

In 1870, the German zoologist Ernst Haeckel gave the word a broader meaning:

> By ecology, we mean the body of knowledge concerning the economy of nature—the investigation of the total relations of the animal both to its organic and to its inorganic environment; including above all, its friendly and inimical relation with those animals and plants with which it comes directly or indirectly into contact—in a word, ecology is the study of all the complex interrelationships referred to by Darwin as the conditions of the struggle for existence.

The word *ecology* came into general use in the late 1800s. Since that time, the science of ecology has grown and diversified. Professional ecologists now number in the tens of thousands and have produced an immense body of knowledge about the world around us. Ecology is an active, modern science that continues to yield fascinating new insights about the environment and our impact on it. As we saw in the chapter opening story about life in the ocean depths, science is an ongoing process through which our understanding of nature constantly changes. Scientific investigation uses a variety of tools to understand how nature works. This understanding is never complete or absolute, but changes constantly as scientists make new discoveries. At the same time, rapid growth of the human population and the increasing sophistication of technological advances have caused major changes in our environment, frequently with dramatic consequences. With the knowledge that ecologists provide through their study of the natural world, we are in a better position to develop effective policies to manage environmental concerns related to land use, water, natural catastrophes, and public health.

This chapter will start you on the road to thinking like an ecologist. Throughout this book, we will consider the full range of **ecological systems**—biological entities that have both their own internal processes and yet interact with their external surroundings. Ecological systems exist at many different levels, ranging from an individual organism to the entire globe. Despite tremendous variations in size, all ecological systems obey the same principles with regard to their physical and chemical attributes and the regulation of their structure and function.

We begin this journey by examining the many different levels of organization for ecological systems, the physical and biological principles that govern ecological systems, and the different roles species play in ecological systems. Once we understand these basics of ecological systems, we will consider the many approaches to studying ecology and then consider the importance of understanding ecology when faced with the wide variety of ways that humans affect ecological systems.

Ecological systems exist in a hierarchy of organization

An ecological system may be an *individual,* a *population,* a *community,* an *ecosystem,* or the entire *biosphere*. As you can see in Figure 1.1, each ecological system is a subset of the next larger one, so the different types of ecological systems form a hierarchy. In this section we will examine the individual components of ecological systems, and how we study ecology at different levels in the ecological hierarchy.

INDIVIDUALS

An **individual** is a living being—the most fundamental unit of ecology. Although smaller units in biology exist—for example an organ, a cell, or a macromolecule—none of them has a separate life in the environment. Every individual has a membrane or other covering across which it exchanges energy and materials with its environment. This boundary separates the internal processes and structures of the ecological system from the external resources and conditions of the environment. In the course of its life, an individual transforms energy and processes materials. To accomplish this, it must acquire energy and nutrients from its surroundings and rid itself of unwanted waste products. This process alters the conditions of the environment and affects the resources available for other organisms. It also contributes to the movement of energy and chemical elements.

POPULATIONS AND SPECIES

Scientists assign organisms to particular *species*. Historically, the term **species** was defined as a group of organisms that naturally interbred with each other and produced fertile offspring. Over time, scientists have realized that this definition does not fit all species because no single definition can apply to all organisms. For example, some species of salamanders

Ecological systems Biological entities that have their own internal processes and interact with their external surroundings.

Individual A living being; the most fundamental unit of ecology.

Species Historically defined as a group of organisms that naturally interbreed with each other and produce fertile offspring. Current research demonstrates that no single definition can be applied to all organisms.

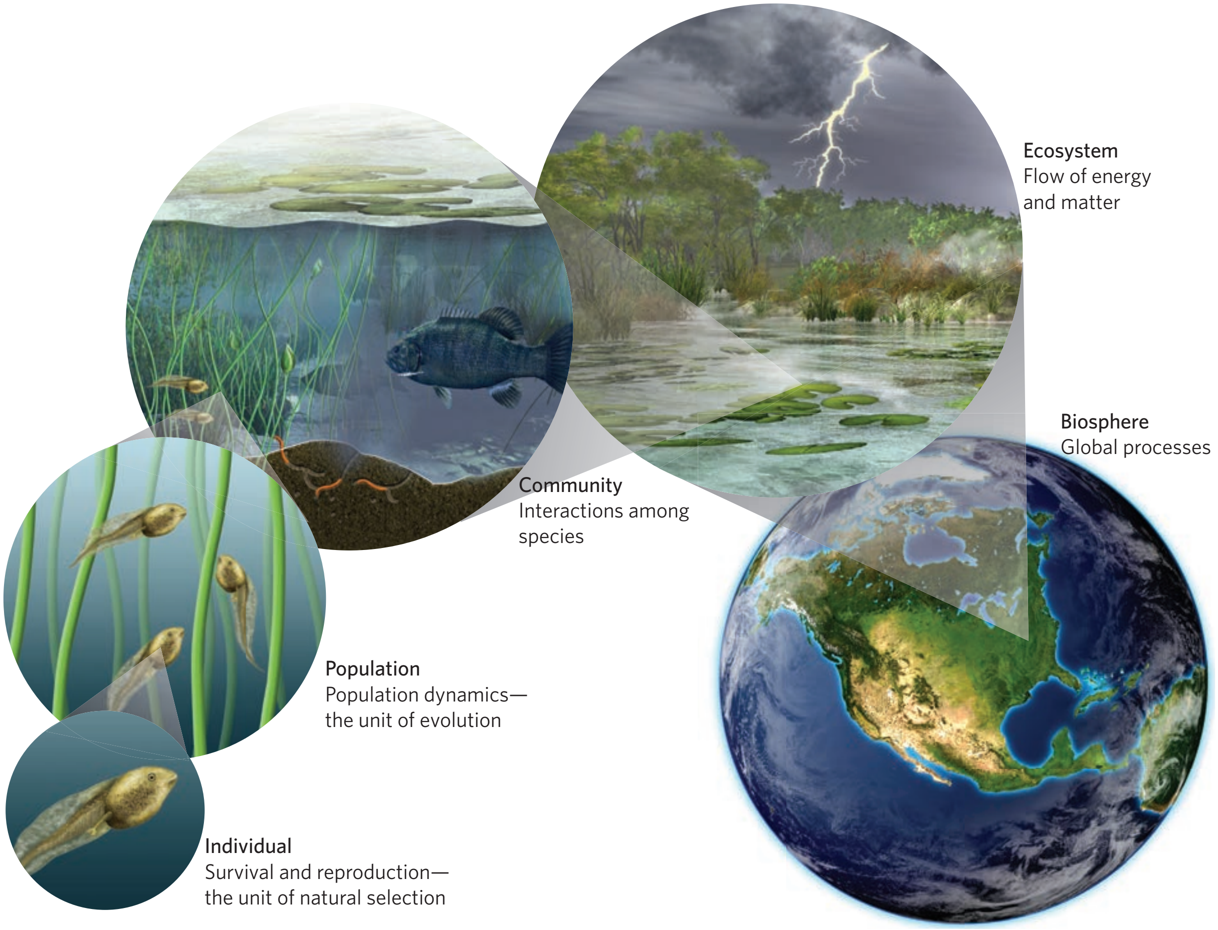


Figure 1.1 The hierarchy of organization in ecological systems. At each level of complexity, ecologists study different processes.

are all female and only produce daughters, which are clones of their mothers. In this case, individuals do not interbreed, but we consider these individuals to be of the same species because they are genetically very similar to each other. In addition, some organisms that we consider distinct species can interbreed. In cases where this interbreeding occurs, we cannot use reproductive isolation to draw the line between species.

Defining a species becomes even more complicated when we consider organisms such as bacteria, which are prokaryotes—that is to say, individuals consisting of a simple, single cell without a nucleus or any other membrane-bound organelles. Scientists increasingly appreciate that prokaryotic organisms can transfer bits of their DNA to other bacteria that are not closely related, a process known as *horizontal gene transfer*. This can happen in a number of ways: when a bacterium engulfs genetic material from the environment, when two bacteria come into contact and exchange genetic material, or when a virus transfers genetic material between two bacteria. Such cases make it difficult to group prokaryotic organisms into distinct species. Despite these difficulties, the term *species* has still proven useful to ecologists.

A **population** consists of individuals of the same species living in a particular area. For example, we might talk about a population of catfish living in a pond, a population of wolves living along the British Columbia coast, or a population of tubeworms living near a hydrothermal vent on the ocean floor. The boundaries that determine a population can be natural, for example where a continent meets the ocean. Alternatively, a population might be defined by another criterion such as a political boundary. For example, a scientist might want to study the coastal population of wolves in British Columbia, whereas biologists with the Canadian Wildlife Service might want to study the wolf population across all of Canada.

Populations have five distinct properties that are not exhibited by individuals: geographic range, abundance, density, change in size, and composition. The *geographic range* of a population—also known as its distribution—is the extent of land or water within which a population lives. For example, the geographic range of the North American grizzly bear (*Ursus*

Population The individuals of the same species living in a particular area.

arctos) includes western Canada, Alaska, Montana, and Wyoming. The *abundance* of a population refers to the total number of individuals. The *density* of a population refers to the number of individuals per unit of area. For instance, we might count the grizzly bears in an area and determine that there is 1 bear/100 km^2. The *change in size* of a population refers to increases and decreases in the number of individuals in an area. Finally, *composition* of a population describes the makeup of the population in terms of gender, age, or genetics. For example, we can ask what proportion of the grizzly population is male versus female, or juvenile versus adult.

COMMUNITIES

At the next level of the ecological hierarchy, we identify an ecological **community**, which is composed of all populations of species living together in a particular area. The populations in a community interact with each other in various ways. Some species eat other species while others, for example bees and the plants they pollinate, have cooperative relationships that benefit both parties. These types of interactions influence the number of individuals in each population. A community may cover large areas, such as a large forest, or may be enclosed within a very small area, such as the community of tiny organisms that live in the digestive systems of animals, or in the tiny amount of water found in tree holes. In practical terms, ecologists who study communities do not study every organism in the community. Instead, they generally study a subset of the organisms in the community, such as the trees, the insects, or the birds, as well as the interactions between certain groups of organisms.

The boundaries that define a community are not always rigid. For example, if you were to examine the species of plants and animals that live at the base of a mountain in Banff National Park in Alberta, you would find that most differ from the species of plants and animals that live at the top of this mountain. That is, the base and the peak appear to have distinctly different communities. However, if you were to walk up the mountain, you would notice that some species of trees, such as Douglas firs (*Pseudotsuga menziesii*), are abundant at the beginning of your hike and then gradually dwindle as you move higher. Other species, such as subalpine firs (*Abies lasiocarpa*), begin to take their place as the number of Douglas firs declines. In other words, the boundaries of the upper and lower forest communities are not distinct. Because of this, scientists must often decide on the boundaries of a community they want to study. For instance, an ecologist might decide to study the community of plants and animals in a section of boreal forest in northern Saskatchewan, or the community of aquatic organisms that lives along a designated stretch of coastline in Labrador. In these cases, no distinct boundary separates the studied community from the area that surrounds it.

ECOSYSTEMS

From communities we move on to *ecosystems*. An **ecosystem** is composed of one or more communities of living organisms interacting with their nonliving physical and chemical environments, which include water, air, temperature, sunlight, and nutrients. Ecosystems are complex ecological systems that can include many thousands of different species living under a great variety of conditions. For example, we may speak of the Great Lakes ecosystem or the boreal forest ecosystem.

At the ecosystem level, we typically focus on the movement of energy and matter between physical and biological components of the ecosystem. Most energy that flows through ecosystems originates with sunlight and eventually escapes Earth as radiated heat. In contrast, matter cycles within and between ecosystems. With the exception of places such as deep-sea vents where energy is acquired through chemosynthesis, the energy for most ecosystems comes from the Sun and is converted to organic compounds by photosynthetic plants and algae. These organisms can then be eaten by *herbivores*—animals that eat plants—which are in turn eaten by *carnivores*—animals that eat other animals. In addition, dead organisms and their waste products can be consumed by *detritivores,* which themselves can be consumed by other animals. In all of these cases, each step results in some of the energy originally assimilated from sunlight being converted into growth or reproduction of consumers; the remainder of the energy is lost to the surroundings as heat, and is eventually radiated back into space.

In contrast to the movement of energy, the movement of matter largely cycles within an ecosystem. When considering matter in an ecosystem, we often look at the most common elements that organisms use, such as carbon, oxygen, hydrogen, nitrogen, and phosphorus. These elements comprise a major portion of the most important compounds for living organisms and include water, carbohydrates, proteins, and DNA. These elements can be held in many different places, or *pools,* on Earth, including in living organisms, and in the atmosphere, water, and rocks. The movement of these elements among these

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Community All populations of species living together in a particular area.

Ecosystem One or more communities of living organisms interacting with their nonliving physical and chemical environments.

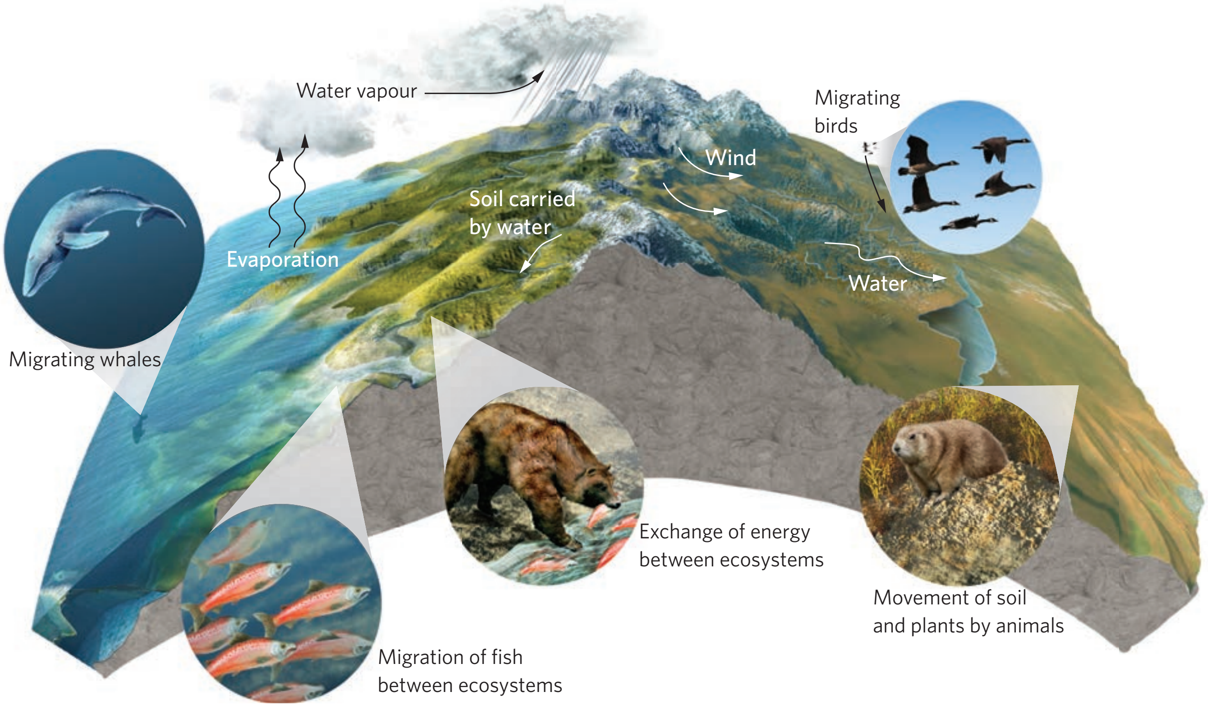

Figure 1.2 The biosphere. The biosphere consists of all ecosystems on Earth, which are linked together by movements of air, water, and organisms.

pools is known as the *flow* of matter. For instance, many nutrients that are in the soil are taken up by plants, and these plants are consumed by animals. The nutrients exist in an animal's tissues, and many leave as excreted waste. When the animal dies, the nutrients in its tissues are returned to the soil, thereby completing the cycling of nutrients.

The boundaries of ecosystems, like those of populations and communities, are often not distinct. Scientists generally distinguish ecosystems by their relative isolation with respect to flows of energy and materials, but, in reality, few ecosystems are completely isolated. Even aquatic and terrestrial ecosystems exchange materials and energy by runoff from the land and the harvesting of aquatic organisms by terrestrial consumers, as when bears capture salmon on their upstream spawning runs.

THE BIOSPHERE

At the highest level of the ecological hierarchy is the **biosphere**, which includes all of the ecosystems on Earth. As Figure 1.2 illustrates, distant ecosystems are linked together by exchanges of energy and nutrients carried by currents of wind and water and by the movements of organisms, such as migrating whales, birds, and fish. Such movement connects terrestrial, freshwater, and marine ecosystems by carrying soil, nutrients, and organisms.

The biosphere is the ultimate ecological system. All transformations of the biosphere are internal, with two exceptions: the energy that enters from the Sun, and the energy that is lost to space. The biosphere holds practically all materials that it has ever had, and retains whatever waste materials we generate.

STUDYING ECOLOGY AT DIFFERENT LEVELS OF ORGANIZATION

Each level in the hierarchy of ecological systems is distinguished by unique structures and processes. As a result, ecologists have developed different approaches for exploring these levels and for answering the questions that arise. The five approaches to studying ecology match the different levels of hierarchy: the *individual approach,* the *population approach,* the *community approach,* the *ecosystem approach,* and the *biosphere approach*.

The **individual approach** to ecology emphasizes the way in which an individual's morphology (the size and shape of its body), physiology, and behaviour enable it to survive in its environment. This approach also seeks to understand why an organism lives in some environments but not in others. For example, an ecologist studying plants at the organism level might

Biosphere All of the ecosystems on Earth.

Individual approach An approach to ecology that emphasizes the way in which an individual's morphology, physiology, and behaviour enable it to survive in its environment.

ask why trees are dominant in warm, moist environments, while shrubs with small, tough leaves are dominant in environments with cool, wet winters and hot, dry summers.

Ecologists who use the individual approach are often interested in **adaptations**—the characteristics of an organism that make it well-suited to its environment. For example, desert animals have enhanced kidney function, which helps them to conserve water. The cryptic colouration of many animals helps them avoid detection by predators. Flowers are shaped and scented to attract certain kinds of pollinators. Adaptations are the result of evolutionary change through the process of *natural selection,* which we will consider later in this chapter.

The **population approach** to ecology examines variation over time and space in the number of individuals, the density of individuals, and the composition of individuals, which includes the sex ratio, the distribution of individuals among different age classes, and the genetic makeup of a population. Changes in the number or density of individuals can reflect the balance of births and deaths within a population, as well as immigration and emigration of individuals from a local population. This can be influenced by a number of factors, including interactions with other species and the physical conditions of the environment, such as temperature or the availability of water. In the process of evolution, genetic mutations may alter birth and death rates, genetically distinct types of individuals may become common within a population, and the overall genetic makeup of the population may change. Because other species might serve as food, pathogens, or predators, interactions among species can also influence the births and deaths of individuals within a population.

The **community approach** to ecology is concerned with understanding the diversity and relative abundances of different kinds of organisms living together in the same place. The community approach focuses on interactions between populations, which can either promote or limit the coexistence of species (Figure 1.3). For example, in studying the Serengeti Plains of Africa, an ecologist taking the community approach might ask how the presence of zebras, which consume grasses, might affect the abundance of other species, such as gazelles, that also consume the grasses.

The **ecosystem approach** to ecology describes the storage and transfer of energy and matter, including the various chemical elements essential to life, such as oxygen, carbon, nitrogen, phosphorus, and sulphur. These movements of energy and matter occur through the activities of organisms and through the physical and chemical transformations that occur in the soil, atmosphere, and water.

Figure 1.3 The community approach to ecology. Ecologists using the community approach study interactions among plants and animals that live together. For example, on an African plain, ecologists might ask how cheetahs (*Acinonyx jubatus*) affect the abundance of gazelles and how the gazelles affect the abundance of the plants that they consume. Photo by Michel & Christine Denis-Huot/Photo Researchers, Inc.

The **biosphere approach** to ecology is concerned with the largest scale in the hierarchy of ecological systems. This approach tackles the movements of air and water—and the energy and chemical elements they contain—over Earth's surface. Ocean currents and winds carry the heat and moisture that define the climates at each location on Earth, which in turn govern the distributions of organisms, the dynamics of populations, the composition of communities, and the productivity of ecosystems.

We have described these five approaches as distinct. However, most ecologists use multiple approaches to study the natural world. A scientist who wants to understand how an ecosystem will respond to a drought, for example, will likely want to know how individual plants and animals respond to a lack of

Adaptation A characteristic of an organism that makes it well-suited to its environment.

Population approach An approach to ecology that emphasizes variation over time and space in the number of individuals, the density of individuals, and the composition of individuals.

Community approach An approach to ecology that emphasizes the diversity and relative abundances of different kinds of organisms living together in the same place.

Ecosystem approach An approach to ecology that emphasizes the storage and transfer of energy and matter, including the various chemical elements essential to life.

Biosphere approach An approach to ecology concerned with the largest scale in the hierarchy of ecological systems, including movements of air and water—and the energy and chemical elements they contain—over Earth's surface.

water, how these individual responses affect the populations of plants and animals, how a change in the populations might affect interactions among species, and how a change in species interactions might affect a change in the flow of energy and matter.

Ecological systems are governed by physical and biological principles

Although ecological systems are complex, they are governed by a few basic principles. Life builds on the physical properties and chemical reactions of matter. The diffusion of oxygen across body surfaces, the rates of chemical reactions, the resistance of vessels to the flow of fluids, and the transmission of nerve impulses all obey the laws of thermodynamics. Within these constraints, life can pursue many options and has done so with astounding innovation. In this section we briefly review the three major biological principles that you may recall from your introductory biology course: *conservation of matter and energy, dynamic steady states,* and *evolution*.

CONSERVATION OF MATTER AND ENERGY

The **law of conservation of matter** states that matter cannot be created or destroyed, but can only change form. For example, as you drive a car, gasoline is burned in the engine; the amount of fuel in the tank declines, but you have not destroyed matter. The molecules that comprise gasoline are converted into new forms including carbon monoxide (CO), carbon dioxide (CO_2), and water (H_2O).

Another important biological principle, the **first law of thermodynamics**—also known as the **law of conservation of energy**—states that energy cannot be created or destroyed. Like matter, energy can only be converted into different forms. Living organisms must constantly obtain energy to grow, maintain their bodies, and replace energy lost as heat.

The law of conservation of matter and the first law of thermodynamics imply that ecologists can track the movement of matter and energy as it is converted into new forms through organisms, populations, communities, ecosystems, and the biosphere. At every level of organization, we should be able to determine how much matter enters the system and account for its movement. For example, consider a field full of cattle (*Bos taurus*) eating grass. At the organismal level, we can determine how much energy an individual animal consumes and then calculate the proportion of this energy that is converted into growth of its body, the maintenance of its physiology, and waste. At the population level, we can calculate how much energy the entire herd of cattle consumes by eating grass. At the community level, we can evaluate how much energy each species of grass creates via photosynthesis and how much of this energy is passed on to cattle and other plant-eating species, such as rabbits that might coexist with the cattle. At the ecosystem level, we can estimate how elements such as carbon flow from the grasses to herbivores (cattle and rabbits) and then on to predators. We can then track how dead grass, the waste products of herbivores and predators, and the dead bodies of herbivores and predators decompose and return to the soil.

DYNAMIC STEADY STATES

Although matter and energy cannot be created or destroyed, ecological systems continuously exchange matter and energy with their surroundings. When gains and losses are in balance, ecological systems are unchanged and the system is said to be in a **dynamic steady state**. For example, birds and mammals continuously lose heat in a cold environment. However, this loss is balanced by heat gained from the metabolism of foods, so the animal's body temperature remains constant. Similarly, the proteins of our bodies are continuously broken down and replaced by newly synthesized proteins, so our appearance remains relatively unchanged.

The principle of the dynamic steady state applies to all levels of ecological organization, as illustrated in Figure 1.4. For individual organisms, assimilated food and energy must balance energy expenditure and metabolic breakdown of tissues. A population increases with births and immigration, and it decreases with death and emigration. At the community level, the number of species living in a community decreases when a species becomes extinct, and increases when a new species colonizes the area. Ecosystems and the biosphere receive energy from the Sun, and this gain of energy is balanced by heat energy radiated by Earth back out into space. One of the most important questions ecologists ask is how the steady states of ecological systems are maintained and regulated. We will return to this question frequently throughout this book.

An understanding of dynamic steady states helps provide insights regarding the inputs and outputs of

Law of conservation of matter Matter cannot be created or destroyed; it can only change form.

First law of thermodynamics Energy cannot be created or destroyed; it can only change form. *Also known as* **Law of conservation of energy**.

Dynamic steady state When the gains and losses of ecological systems are in balance.

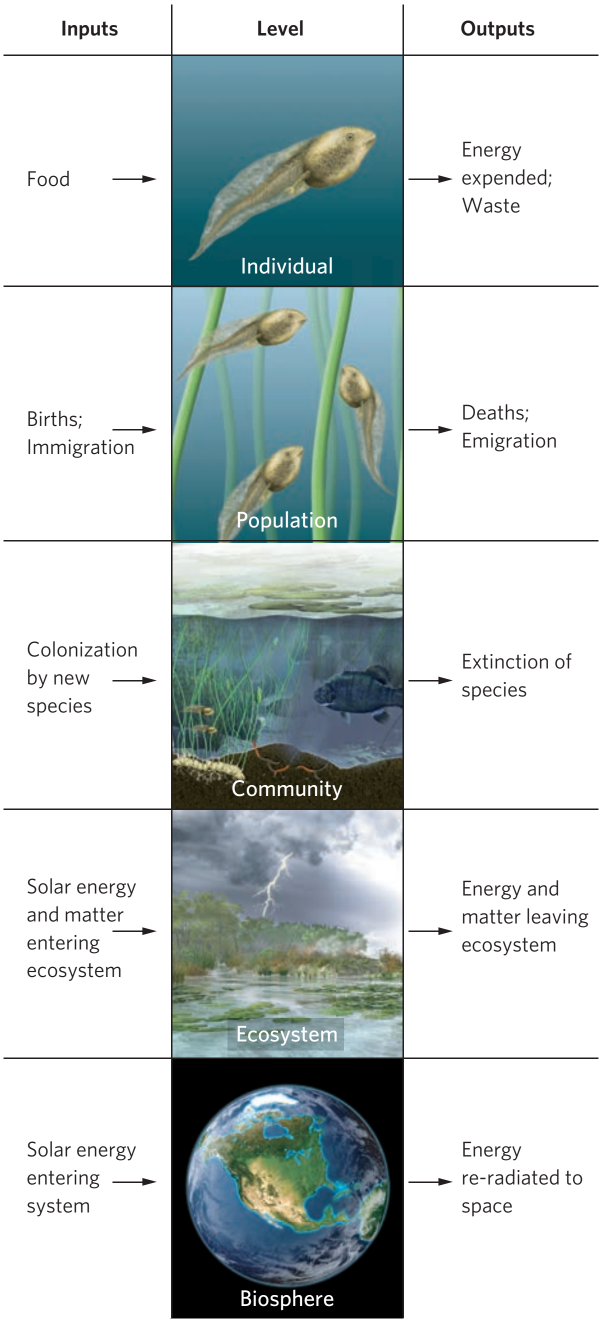

Figure 1.4 Dynamic steady states. At all levels of organization, the inputs to the systems must equal the outputs.

ecological systems. Of course, ecological systems also change. Organisms grow, populations vary in abundance, and abandoned fields revert to forest. Yet all ecological systems have mechanisms that tend to maintain a dynamic steady state.

EVOLUTION

Although matter and energy cannot be created or destroyed, what living systems do with matter and energy is as variable as all the forms of organisms that have ever existed on Earth. To understand the variation among organisms—the diversity of life—we turn to the concept of *evolution*.

An attribute of an organism, such as its behaviour, morphology, or physiology, is the organism's **phenotype**. A phenotype is determined by the interaction of the organism's **genotype**, or the set of genes it carries, with the environment in which it lives. For example, your height is a phenotype that is determined by your genes and the nutrition you received in the environment where you were raised.

Over the history of life on Earth, the phenotypes of organisms have changed and diversified dramatically. This is the process of **evolution**, which is a change in the genetic composition of a population over time. Evolution can happen through a number of different processes that we will discuss in detail in later chapters. Perhaps the best known process is evolution by **natural selection**, which is a change in the frequency of genes in a population through differential survival and reproduction of individuals that possess certain phenotypes. As outlined by Charles Darwin in his book *On the Origin of Species*, evolution by natural selection depends on three conditions:

1. Individual organisms vary in their traits.
2. Parental traits are inherited by their offspring.
3. The variation in traits causes some individuals to experience higher **fitness**, which we define as the survival and reproduction of an individual.

When these three conditions exist, an individual with higher survival and reproductive success will pass more copies of its genes to the next generation. Over time, the genetic composition of a population changes as the most successful phenotypes come to predominate. As a result, the population becomes better suited to the surrounding environmental conditions. Phenotypes that are well suited to their environment and, in turn, confer higher fitness are known as adaptations. Consider the example in

Phenotype An attribute of an organism, such as its behaviour, morphology, or physiology.

Genotype The set of genes an organism carries.

Evolution Change in the genetic composition of a population over time.

Natural selection Change in the frequency of genes in a population through differential survival and reproduction of individuals that possess certain phenotypes.

Fitness The survival and reproduction of an individual.