3

Native Hawaiian forest at Hakalau Forest NWR, and the endangered 'akiapōlā'au

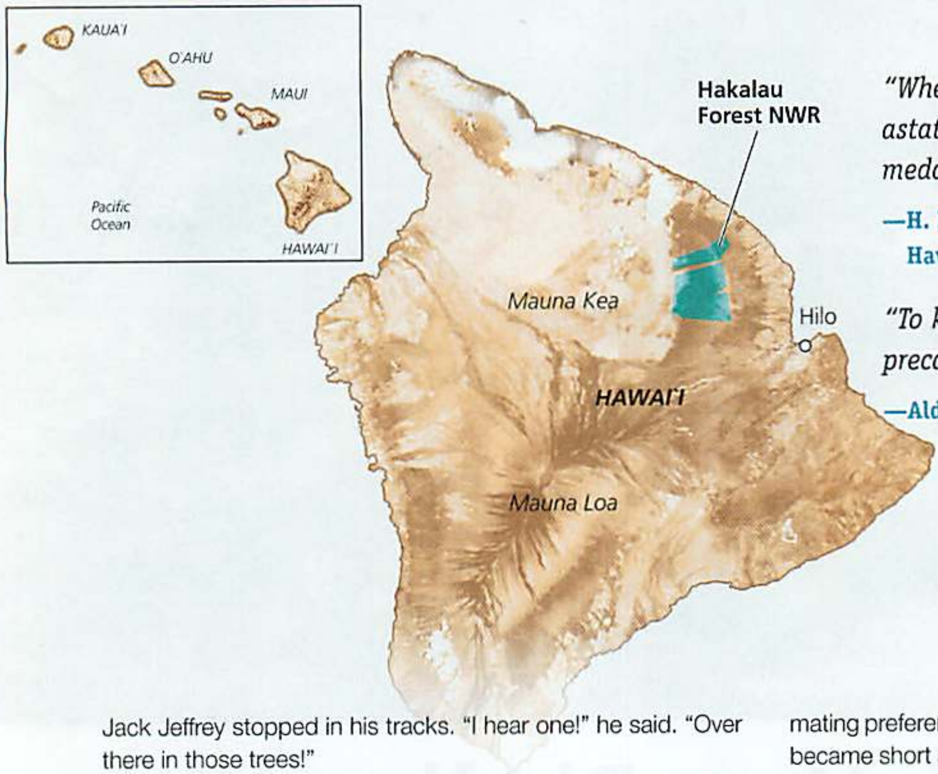
Evolution, Biodiversity, and Population Ecology

Upon completing this chapter, you will be able to:

- Explain natural selection and cite evidence for this process
- Describe how evolution influences biodiversity
- Discuss reasons for species extinction and mass extinction events
- List the levels of ecological organization
- Outline the characteristics of populations that help predict population growth
- Assess logistic growth, carrying capacity, limiting factors, and other fundamental concepts in population ecology
- Identify efforts and challenges involved in the conservation of biodiversity

CENTRAL CASE STUDY

Saving Hawaii's Native Forest Birds



"When an entire island avifauna . . . is devastated almost overnight because of human meddling, it is, quite simply, a tragedy."

—H. Douglas Pratt, ornithologist and expert on Hawaiian birds

"To keep every cog and wheel is the first precaution of intelligent tinkering."

—Aldo Leopold

Jack Jeffrey stopped in his tracks. "I hear one!" he said. "Over there in those trees!"

Jeffrey quickly led his group of ecotourists through a misty woodland of ferns, grasses, koa trees, and red-flowering ‘ōhi‘a-lehua trees toward an emphatic chirping sound that carried farther than the other bird songs in the forest. At last they spotted the bird—an ‘akiapōlā‘au, one of fewer than 1500 of its kind left alive in the world.

The ‘akiapōlā‘au (or "aki" for short) is a sparrow-sized wonder of nature—one of many exquisite birds that evolved on the Hawaiian Islands and exists only here. For millions of years, this chain of islands in the middle of the Pacific Ocean has acted as a cradle of evolution, generating an abundance of new and unique species. Yet in recent years, many of these species have gone from cradle to grave. Half of Hawaii's native bird species (70 of 140) have gone extinct in recent times, and the percentage of species that teeter on the brink of extinction here today is higher than anywhere else in the world.

The aki is one of 30 species of endangered birds remaining on the Hawaiian Islands. It is a type of Hawaiian honeycreeper, a group of birds numbering 18 living species (and at least 38 species recently extinct), all of which originated from individuals of a single ancestral species that reached Hawai‘i several million years ago. As new volcanic islands emerged from the ocean and then eroded away, and as forests expanded and contracted over the millennia, populations were split many times, and new honeycreeper species evolved.

As honeycreeper species diverged from one another, they evolved different colors, sizes, body shapes, feeding behaviors, mating preferences, diets, and bill shapes. Bills in some species became short and straight, allowing birds to glean insects from leaf surfaces. In other species, bills became long and downcurved, enabling birds to probe into flowers to sip nectar. The bills of still other species became thick and strong for cracking seeds. Some bills became highly specialized: The aki uses the short, straight lower half of its bill to peck, woodpecker-style, into dead twigs and branches of koa trees to find beetle grubs, and then uses the long, downcurved upper half to reach in and extract the grubs.

Hawaii's honeycreepers thrived for several million years in the island's forests, amid a unique community of plants. The stately ‘ōhi‘a, a slow-growing tree that can live for 2000 years, spreads twisting gnarled limbs covered with moss and lichens through the misty air, and offers up bright red flowers that provide nectar and pollen to birds and insects. The koa thrives here too, a fast-growing acacia tree with twigs that the aki snaps off in its search for grubs. A multitude of shrubs, herbs, and vines found nowhere else in the world used to fill out the forest understory.

Today native Hawaiian forests are under siege. The crisis began several hundred years ago when Polynesian settlers colonized the islands, cutting down trees and introducing nonnative animals. Europeans arrived in the 1800s and did more of the same. Pigs, goats, and cattle ate their way through the native plants, transforming lush forests into ragged grasslands. Rats, cats, dogs, and mongooses destroyed the eggs and young of native ground-nesting birds. Foreign plants from Asia, Europe, and America, whose seeds accompanied the people and animals, spread across the altered landscape.

The newly introduced organisms wreaked havoc because native Hawaiian organisms were unprepared to resist them. Hawai'i is so isolated that only one mammal—a bat—had ever arrived naturally. As a result, plants had faced no pressure to invest in defenses (such as thick bark, spines, or chemical toxins) against plant-eating livestock. Likewise, nothing had led birds to evolve defenses against voracious nest predators such as rats and mongooses. The vulnerable native species were easy pickings, and many were soon wiped off the face of the planet.

With the arrival of people, domestic animals, and invasive plants also came diseases. The native fauna were not adapted to resist diseases they had never encountered. Avian pox and avian malaria spread through Hawaii's birds. Malaria and the mosquitoes that carry the disease killed off the natives everywhere except on the high slopes of the mountains, where it becomes too cold for the malaria parasite to survive. Today few native forest birds exist anywhere on the Hawaiian Islands below 1500 m (4500 ft) in elevation.

The aki being watched by Jack Jeffrey's group inhabits the Hakalau Forest National Wildlife Refuge, which sits high on the slopes of Mauna Kea, a volcano on the island of Hawai'i, the largest island in the chain. At Hakalau, native birds find one of the few remaining patches of malaria-free native forest on the island.

Conservation biologists and managers have worked hard to keep the Hakalau Forest protected. Jack Jeffrey was the refuge biologist here for 20 years, and led a number of innovative projects to save native plants and birds from extinction. Managers at Hakalau have fenced out pigs to safeguard forested areas, and refuge staff and volunteers have planted thousands of native plants in areas deforested by cattle grazing. Young restored native forest is now regrowing on thousands of acres. More birds are using this restored forest year by year.

Today global climate change is throwing up a new challenge. As temperatures warm, mosquitoes move upslope, and malaria and pox spread deeper into the remaining forests, so that even protected areas such as Hakalau are not immune. The next generation of managers will need to innovate novel strategies to fend off extinction for the island's native species.

Plenty of challenges remain, but the restoration successes at Hakalau Forest so far provide hope that through responsible management we can save Hawaii's native flora and fauna and preserve the priceless bounty of millions of years of evolution on this extraordinary chain of islands. ●

Evolution: The Source of Earth's Biodiversity

The honeycreepers and the other native animals and plants of Hawai'i help reveal how our world became populated with the remarkable diversity of life we see today. Scientific study shows us that our planet has progressed from a stark world inhabited solely by microbes to a lush cornucopia of millions of species (**FIGURE 3.1**).

A **species** is a particular type of organism or, more precisely, a population or group of populations whose members share characteristics and can freely breed with one another and produce fertile offspring. A **population** is a group of individuals of a particular species that live in a particular area. Over vast spans of time, the process of biological evolution

(a) 'I'iwi (*Vestiaria coccinea*)

(b) Nēnē (*Branta sandvicensis*)

(c) Haleakala silversword (*Argyroxiphium sandwichense*)

(d) Happyface spider (*Theridion grallator*)

FIGURE 3.1 Hawai'i hosts a treasure trove of biological diversity.

has shaped populations and species, giving us the vibrant abundance of life that enriches Earth today.

Evolution in the broad sense means change over time, and biological evolution consists of change in populations of organisms across generations. Changes in genes (p. 29) often lead to modifications in the appearance or behavior of organisms from generation to generation. Biological evolution results from random genetic changes and may be directed by natural selection. **Natural selection** is the process by which inherited characteristics that enhance survival and reproduction are passed on more frequently to future generations than those that do not, thus altering the genetic makeup of populations through time.

Evolution is one of the best-supported and most illuminating concepts in all of science, and it is the very foundation of modern biology. Perceiving how species adapt to their environments and change over time is crucial for comprehending ecology and learning the history of life. Evolutionary processes influence many aspects of environmental science, including pesticide resistance, agriculture, medicine, and environmental health.

Natural selection shapes organisms and diversity

In 1858, **Charles Darwin** and **Alfred Russel Wallace** each independently proposed the concept of natural selection as a mechanism for evolution and as a way to explain the great variety of living things. Both Darwin and Wallace were exceptionally keen naturalists from England who had studied plants and animals in such exotic locales as the Galápagos Islands (Darwin) and the Malay Archipelago (Wallace). In the century and a half since then, many thousands of scientists have refined our understanding of natural selection and evolution.

Natural selection is a simple concept that offers a powerful explanation for patterns evident in nature. The idea of natural selection follows logically from a few straightforward premises that are readily apparent to anyone who observes the life around us:

- Organisms face a constant struggle to survive and reproduce.
- Organisms tend to produce more offspring than can survive.
- Individuals of a species vary in their characteristics.

Variation is due to differences in genes, the environments in which genes are expressed, and the interactions between genes and environment. As a result of this variation, some individuals of a species will be better suited to their environment than others and will be better able to reproduce.

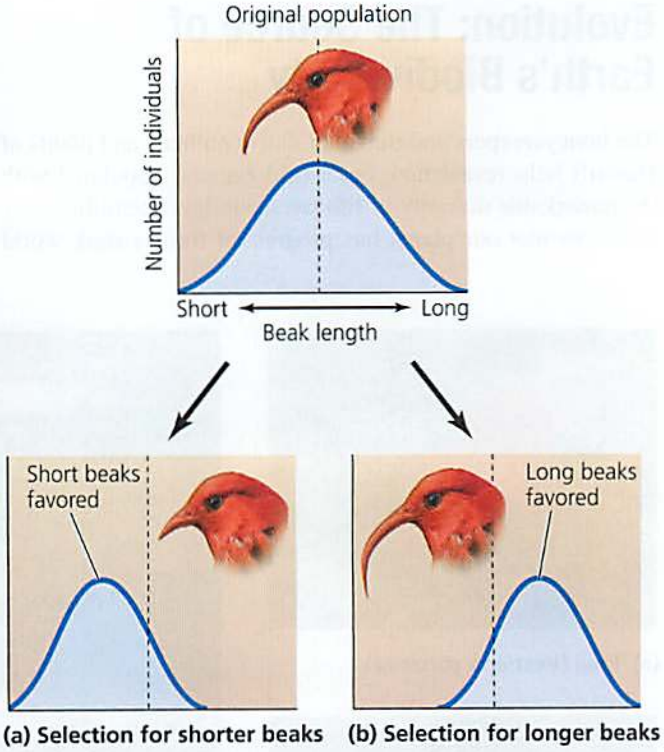
Many characteristics are passed from parent to offspring through the genes, and a parent that produces many offspring will pass on more genes to the next generation than a parent that produces few or no offspring. In the next generation, therefore, the genes of better-adapted individuals will outnumber those of individuals that are less well adapted. From one generation to another through time, characteristics, or traits, that lead to better and better reproductive success in a given environment will evolve in the population. This process is termed **adaptation,** and a trait that promotes success is also called an **adaptation** or an **adaptive trait.**

Selection acts on genetic variation

For an organism to pass a trait along to future generations, genes in the organism's DNA (p. 29) must code for the trait. In an organism's lifetime, its DNA will be copied millions of times by millions of cells. In all this copying and recopying, sometimes a mistake is made. Accidental changes in DNA, called **mutations,** give rise to genetic variation among individuals. If a mutation occurs in a sperm or egg cell, it may be passed on to the next generation. Most mutations have little effect, but some can be deadly, whereas others can be beneficial. Those that are not lethal provide the genetic variation on which natural selection acts.

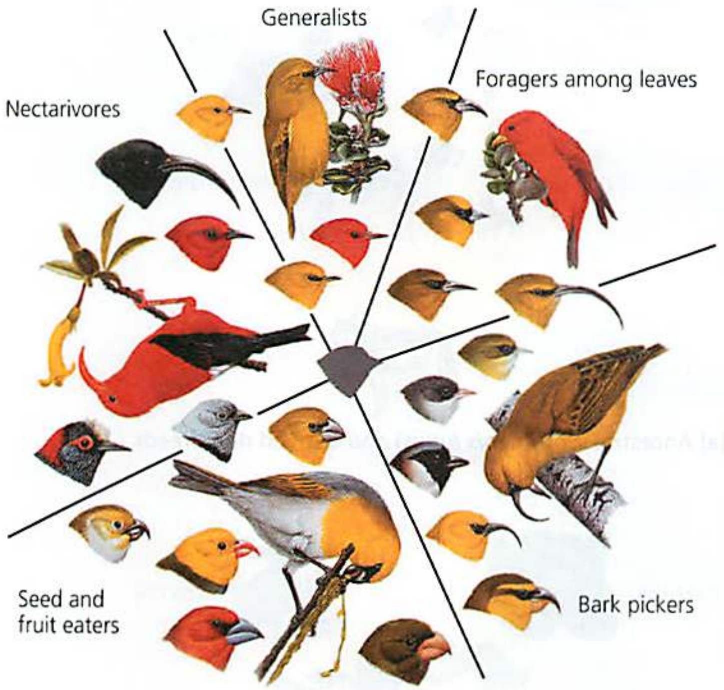
Genetic variation is also generated as organisms mix their genetic material through *recombination* during sexual reproduction. When organisms reproduce sexually, a portion of each parent's genes contributes to the genes of the offspring. This process produces novel combinations of genes, generating variation among individuals.

When natural selection acts on genetic variation by favoring certain variants, it can drive a feature in a particular direction (**FIGURE 3.2**). Because such evolutionary change



(a) Selection for shorter beaks **(b) Selection for longer beaks**

FIGURE 3.2 Natural selection can drive a feature in various directions. Let's consider the 'i'iwi, a Hawaiian honeycreeper, and assume its population possesses genetic variation for the length of its curved bill. In an environment where flowers grow shorter nectar tubes **(a)**, birds with shorter bills could feed perfectly well and could avoid investing in a long bill, so natural selection would favor a decrease in bill length across the population. But in an environment where flowers have longer tubes **(b)**, birds with longer bills could feed more effectively and pass on more genes, causing the population to shift toward a longer average bill length.



(a) Divergent evolution of Hawaiian honeycreepers

(b) Convergent evolution of a cactus in Arizona (top) and a euphorb (spurge) in the Canary Islands (bottom)

FIGURE 3.3 Natural selection can cause closely related species to diverge in appearance or distantly related species to converge in appearance. Hawaiian honeycreepers **(a)** diversified as they adapted to different food resources and habitats, as indicated by the diversity of their plumage colors and bill shapes. In contrast, cacti of the Americas and euphorbs of Africa **(b)** became more similar to one another as they independently adapted to arid environments through the evolution of tough succulent tissues to hold water, thorns to keep thirsty animals away, and photosynthetic stems without leaves to reduce surface area and water loss.

generally requires a great deal of time, a species cannot always adapt to environmental conditions that change quickly. For instance, the warming of our global climate today (Chapter 18) is occurring too rapidly for most species to adapt, and we may lose many species to extinction as a result.

However, genetic variation can sometimes help protect a population against novel challenges. One of the honeycreeper species of the Hakalau Forest, the ʻamakihi, has in recent years been discovered in ʻōhiʻa trees at very low elevations, well within the zone where avian malaria has killed off all other honeycreepers. Researchers studying this population have determined that some of the ʻamakihis living here when malaria arrived had genes that by chance gave them a natural resistance to the disease. These resistant birds survived malaria's onslaught, and their descendants reestablished a population that continues to grow today. Similarly, the ʻapapane (another Hawaiian honeycreeper) and the ʻōmaʻo (a native Hawaiian thrush) also are showing some degree of resistance to malaria. Scientists hope that perhaps some individuals of the rarer native birds of Hakalau might also harbor resistance genes that may help them persist in the face of malaria.

Selective pressures from the environment influence adaptation

Environmental conditions determine what pressures natural selection will exert, and these selective pressures affect which members of a population will survive and reproduce. Over many generations, this results in the evolution of traits that enable success within the environment in question. Closely related species that live in very different environments and thus experience very different selective pressures tend to diverge in their traits as the differing pressures drive the evolution of different adaptations (**FIGURE 3.3a**). Conversely, sometimes very unrelated species may acquire similar traits as they adapt to selective pressures from similar environments; this is called **convergent evolution** (**FIGURE 3.3b**).

However, environments change over time, and organisms may move to new locations and encounter new conditions. In either case, a trait that promotes success at one time or place may not do so at another. Hawaiian honeycreepers such as the ʻapapane and the ʻiʻiwi fly long distances in search of flowering trees. This behavior had long helped them to find the best resources across a diverse landscape. However, once malaria arrived, the strategy backfired, as birds from malaria-free areas would sometimes fly into death zones. Today, thousands of honeycreepers from mountain forests die each year when they fly downslope and are bitten by malarial mosquitoes. As environmental conditions vary in time and space, adaptation becomes a moving target.

FAQ **Isn't evolution based on just one man's beliefs?**

Because Charles Darwin contributed so much to our early understanding of evolution, many people assume the concept itself hinges on his ideas. But scientists and laypeople had been observing nature and puzzling over fossils for a long time, and the notion of evolution was being discussed long before Darwin. Once he and Alfred Russel Wallace independently proposed the concept of natural selection, scientists finally gained a precise and feasible mechanism to explain how and why organisms change across generations. Later, geneticists discovered Gregor Mendel's research and worked out how traits are inherited—and modern evolutionary biology was born. Twentieth-century scientists Fisher, Wright, Dobzhansky, Simpson, Mayr, and others ran experiments and developed sophisticated mathematical models, documenting phenomena with extensive evidence and making evolutionary biology into one of science's strongest fields. Since then, evolutionary research by thousands of scientists has driven our understanding of biology and has facilitated spectacular advances in agriculture, medicine, and biotechnology.

Evidence of selection is all around us

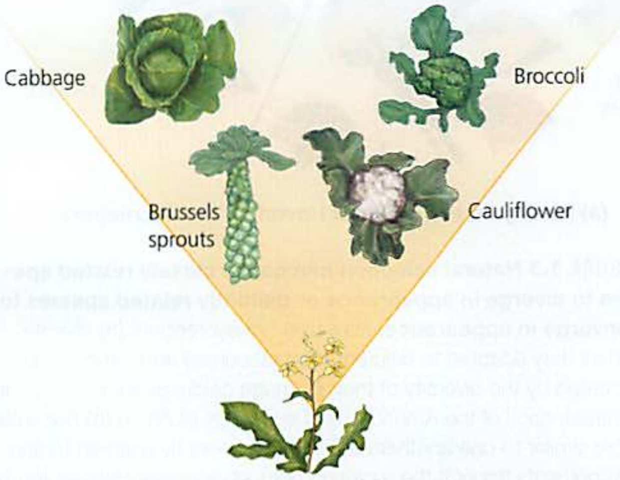
The results of natural selection are all around us, visible in every adaptation of every organism. In addition, scientists have demonstrated the rapid evolution of traits by selection in countless lab experiments, mostly with fast-reproducing organisms such as bacteria, yeast, and fruit flies.

The evidence for selection that may be most familiar to us is that which Darwin himself cited prominently in his work 150 years ago: our breeding of domesticated animals. In domesticated dogs, cats, and livestock, we have conducted selection under our own direction. We have chosen animals with traits we like and bred them together, while not breeding those with variants we do not like. Through such *selective breeding*, we have been able to augment particular traits we prefer.

Consider the great diversity of dog breeds (FIGURE 3.4a). People generated every type of dog alive today by starting with a single ancestral species and selecting for particular desired traits as individuals were bred together. From Great Dane to Chihuahua, all dogs are able to interbreed and produce viable offspring, yet breeders maintain striking differences among them by allowing only like individuals to breed with like. This process of selection conducted under human direction is termed **artificial selection.**

Artificial selection has given us the many crop plants we depend on for food, all of which people domesticated from wild ancestors and carefully bred over years, centuries, or millennia (FIGURE 3.4b). Through selective breeding, we have created corn with bigger, sweeter kernels; wheat and rice with larger and more numerous grains; and apples, pears, and oranges with better taste. We have diversified single types into many—for instance, breeding variants of the plant *Brassica oleracea* to create broccoli, cauliflower, cabbage, and brussels sprouts. Our entire agricultural system is based on artificial selection. We depend on a working understanding of evolution for the very food we eat.

(a) Ancestral wolf (*Canis lupus*) and derived dog breeds



(b) Ancestral *Brassica oleracea* and derived crops

FIGURE 3.4 Selective breeding, or artificial selection, has resulted in our many breeds of dogs and varieties of crops. With dogs **(a)**, we began with the gray wolf *(Canis lupus)* as the ancestral wild species, and by breeding like with like and selecting for the traits we prefer, we have produced breeds as different as Great Danes and Chihuahuas. By this same process we have created our immense variety of crop plants **(b)**. Cabbage, brussels sprouts, broccoli, and cauliflower were all generated from a single ancestral species, *Brassica oleracea*.

Evolution generates biodiversity

Just as artificial selection helps us create new types of pets, farm animals, and crop plants, natural selection serves to elaborate and diversify traits in wild organisms. Over the long term, natural selection helps lead to the formation of new species and whole new types of organisms. Life's complexity can be expressed as **biological diversity,** or **biodiversity** for short, which refers to the variety of life across all levels of biological organization, including the diversity of species, genes, populations, and communities (we will introduce communities shortly: p. 60 and Chapter 4).

Scientists have described about 1.8 million species, but many more remain undiscovered or unnamed. Estimates for the total number of species in the world vary, but they range from 3 million up to 100 million. Hawaii's insect fauna provides one example of how much we have yet to learn. Scientists studying fruit flies in the Hawaiian Islands have described over 500 species of them, but they have also identified about 500 others that have not yet been formally named and described. Still more fruit fly species probably exist but have not yet been found.

Subtropical islands such as Hawai'i are by no means the only places rich in biodiversity, however. Step outside anywhere, and you will find many species within close reach. They may not always be large and conspicuous like Yellowstone's bears or the Serengeti's elephants, but they will be there. Plants poke up from cracks in asphalt in every city in the world, and even Antarctic ice harbors microbes. A handful of backyard soil may contain an entire miniature world of life, including insects, mites, millipedes, nematode worms, plant seeds, fungi, and millions upon millions of bacteria. (We will examine Earth's biodiversity in detail in Chapter 11.)

Speciation produces new types of organisms

How did Earth come to have so many species? The process by which new species are generated is termed **speciation.** Speciation can occur in a number of ways, but the main mode is generally thought to be *allopatric speciation*, whereby species form from populations that become physically separated over some geographic distance. To understand allopatric speciation, begin by picturing a population of organisms. Individuals within the population possess many similarities that unify them as a species because they are able to breed with one another and share genetic information. However, if the population is broken up into two or more isolated areas, individuals from one area cannot reproduce with individuals from the others.

When a mutation arises in the DNA of an organism in one of these newly isolated populations, it cannot spread to the other populations. Over time, each population will independently accumulate its own set of mutations. Eventually, the populations may diverge, growing so different that their members can no longer mate with one another. Once this has happened, there is no turning back; the two populations can no longer share genetic information, and they will embark on their own independent evolutionary trajectories as separate species (**FIGURE 3.5**). The populations will continue diverging in their characteristics as chance mutations accumulate that cause them to differ more and more. If environmental conditions happen to differ for the two populations, then natural selection may accelerate the divergence.

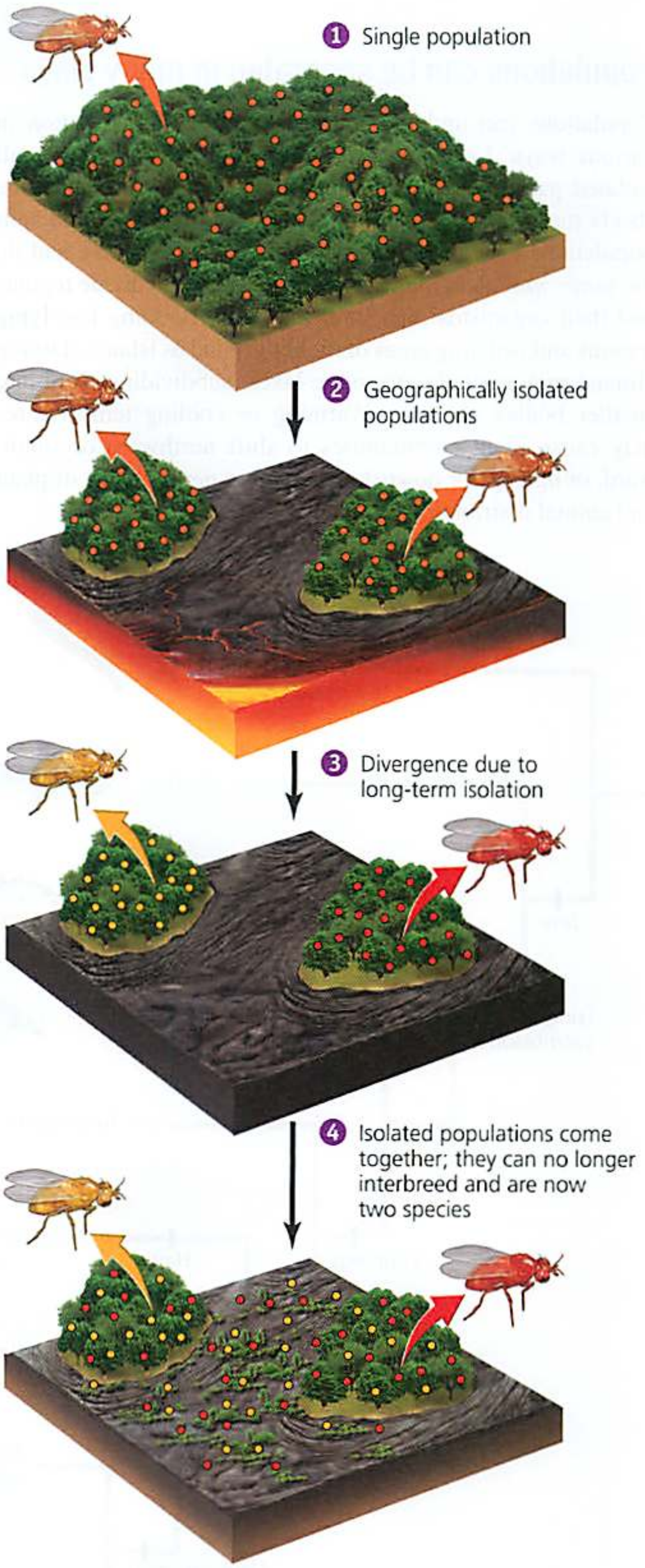


FIGURE 3.5 In allopatric speciation, species form from populations that become physically separated over some geographic distance. This long, slow process begins when a geographic barrier splits a population—as when forest ① is destroyed by lava flowing from a volcano but isolated patches of forest ② are left. In Hawai'i such forested patches are called *kipukas*. Hawaiian fruit flies are weak fliers and become isolated in kipukas. Over the centuries, each population accumulates its own independent set of genetic changes ③, until individuals become genetically distinct from and unable to breed with individuals from the other population. The two populations now represent separate species and will remain so even when the geographic barrier disappears ④, new forest grows over the eroding lava rock, and the new species intermix.

Populations can be separated in many ways

Populations can undergo long-term geographic isolation in various ways. Lava flows can destroy forest, leaving small isolated patches intact (as shown in Figure 3.5). Glacial ice sheets may move across continents during ice ages and split populations in two. Major rivers may change course and do the same. Mountain ranges may be uplifted and divide regions and their organisms. Sea level may rise, flooding low-lying regions and isolating areas of higher ground as islands. Drying climate may partially evaporate lakes, subdividing them into smaller bodies of water. Warming or cooling temperatures may cause plant communities to shift northward or southward, or upslope or downslope, creating new patterns of plant and animal distribution.

Alternatively, sometimes new areas are created and organisms colonize them, establishing isolated populations. Hawai'i provides an example. As shown in Figure 2.22 (Chapter 2, p. 41), the Pacific tectonic plate moves over a volcanic "hotspot" that extrudes magma into the ocean, building volcanoes that form islands once they break the water's surface. The plate inches northwest, dragging each island with it, while new islands are formed at the hotspot. The result, over millions of years, is a long string of islands, an *archipelago*. As each new island is formed, plants and animals that colonize it may undergo allopatric speciation if they are isolated enough from their source population (see **THE SCIENCE BEHIND THE STORY**, pp. 56–57).

For speciation to occur, populations must remain isolated for a very long time, generally thousands of generations. Then, if the geologic or climatic process that has isolated populations reverses itself—if the glacier recedes, or the river returns to its old course, or warm temperatures turn cool again—then the populations may come back together. This is the moment of truth for speciation. If the populations have not diverged enough, their members will begin interbreeding and reestablish gene flow, mixing the mutations that each population accrued while isolated. However, if the populations have diverged sufficiently, they will not interbreed, and two species will have been formed, each destined to continue on its own evolutionary path.

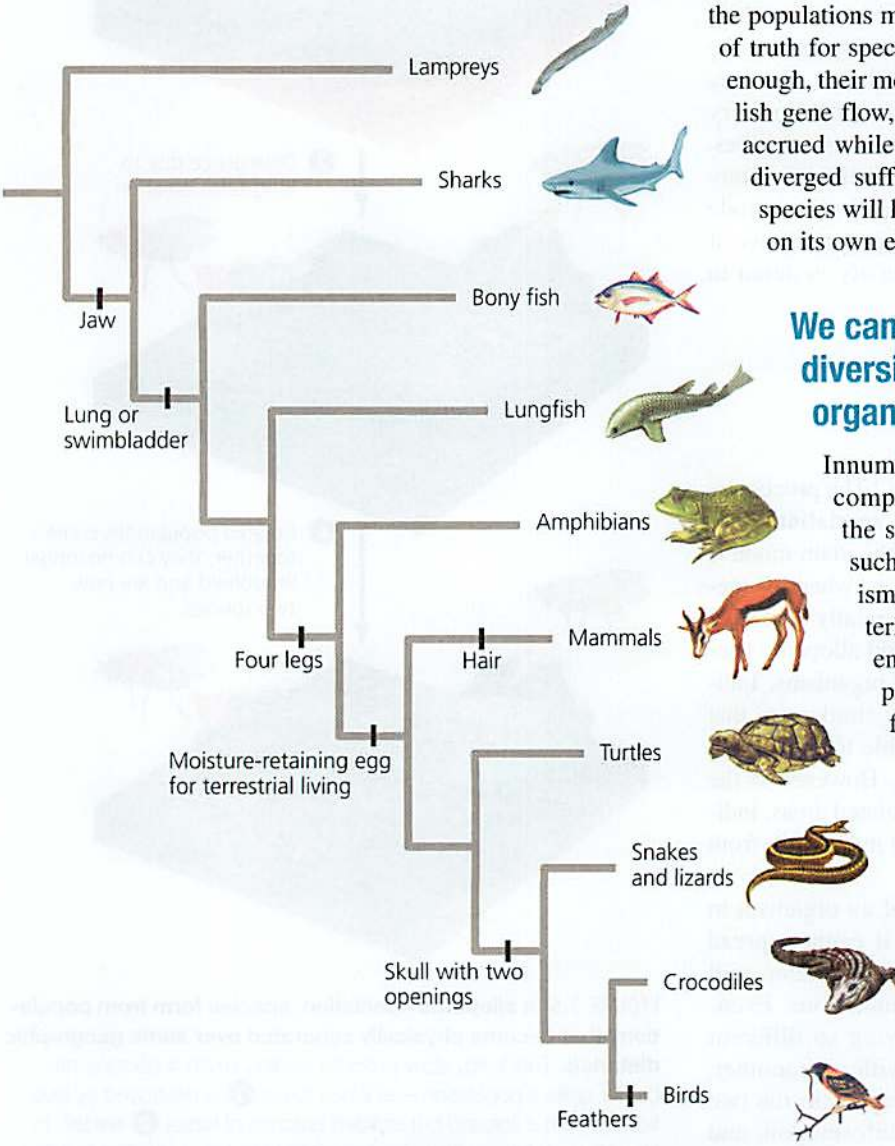


FIGURE 3.6 **Phylogenetic trees show the history of life's divergence.** The tree here illustrates relationships among groups of vertebrates—just one small portion of the huge and complex "tree of life." Each branch results from a speciation event; as you follow the tree left to right from its trunk to the tips of its branches, you proceed forward in time, tracing life's history. In this tree, major traits are "mapped" on to indicate when they originated. For instance, all vertebrates to the right of the hash mark indicating the origin of jaws possess jaws, whereas lampreys diverged before jaws originated and thus lack them.

We can infer the history of life's diversification by comparing organisms

Innumerable speciation events have generated complex patterns of diversity at levels above the species level. Evolutionary biologists study such patterns, examining how groups of organisms arose and how they evolved the characteristics they show. For instance, how did we end up with plants as different as mosses, palm trees, daisies, and redwoods? Why do fish swim, snakes slither, and sparrows sing? How and why did birds, bats, and insects each independently evolve the ability to fly? To address such questions, we need to know how the major groups diverged from one another over time.

Scientists represent this history of divergence by using branching, treelike diagrams called **phylogenetic trees.** Similar to family genealogies, these diagrams illustrate scientists' hypotheses as to how divergence took place (**FIGURE 3.6**). Phylogenetic trees can show relationships among species, groups of species, populations, or genes. Scientists construct these trees by analyzing patterns of similarity among the genes or external traits of present-day organisms and by inferring which groups share similarities because they are related.

Once we have a phylogenetic tree, we can map traits onto the tree according to which organisms possess them, and we can thereby trace how the traits have evolved. For instance, phylogenetic research shows that birds, bats, and insects are distantly related, with many flightless groups between them. (Note in Figure 3.6 that birds and mammals are separated on the tree and that insects are outside the tree.) Therefore, it is far simpler to conclude that these three very different groups evolved flight independently than it would be to conclude that the many flightless groups between them each lost an ancestral ability to fly. Because phylogenetic trees help biologists make such inferences about so many traits, they have become one of the modern biologist's most powerful tools.

Knowing how organisms are related to one another also helps scientists to classify them and name them, so that we can make sense of the life around us and communicate effectively. *Taxonomists* use an organism's physical appearance and genetic makeup to determine its species. These scientists then group species by their similarity into a hierarchy of categories meant to reflect evolutionary relationships. Related species are grouped together into *genera* (singular, *genus*), related genera are grouped into families, and so on (**FIGURE 3.7**). Each species is given a two-part Latin or Latinized scientific name denoting its genus and species.

For instance, the ‘akiapōlā‘au, *Hemignathus munroi*, is similar to other Hawaiian honeycreepers in the genus *Hemignathus*. These species are closely related in evolutionary terms, as indicated by the genus name they share. They are more distantly related to honeycreepers in other genera, but all honeycreepers are classified together in the family Fringillidae. This system of naming and classification was devised by Swedish botanist Carl Linnaeus (1707–1778) long before Darwin's work on evolution. Today biologists use evolutionary information from phylogenetic trees to help classify organisms under the Linnaean system's rules.

The fossil record teaches us about life's long history

Scientists also decipher life's history by studying fossils. As organisms die, some are buried by sediment. Under certain conditions, the hard parts of their bodies—such as bones, shells, and teeth—may be preserved, as sediments are compressed into rock (pp. 37–38). Minerals replace the organic material, leaving behind a **fossil**, an imprint in stone of the dead organism (**FIGURE 3.8**, p. 58). In countless locations throughout the world, geologic processes across millions of years have buried sediments and later brought sedimentary rock layers to the surface, revealing assemblages of fossilized plants and animals from different time periods. By dating the rock layers that contain fossils, paleontologists (scientists

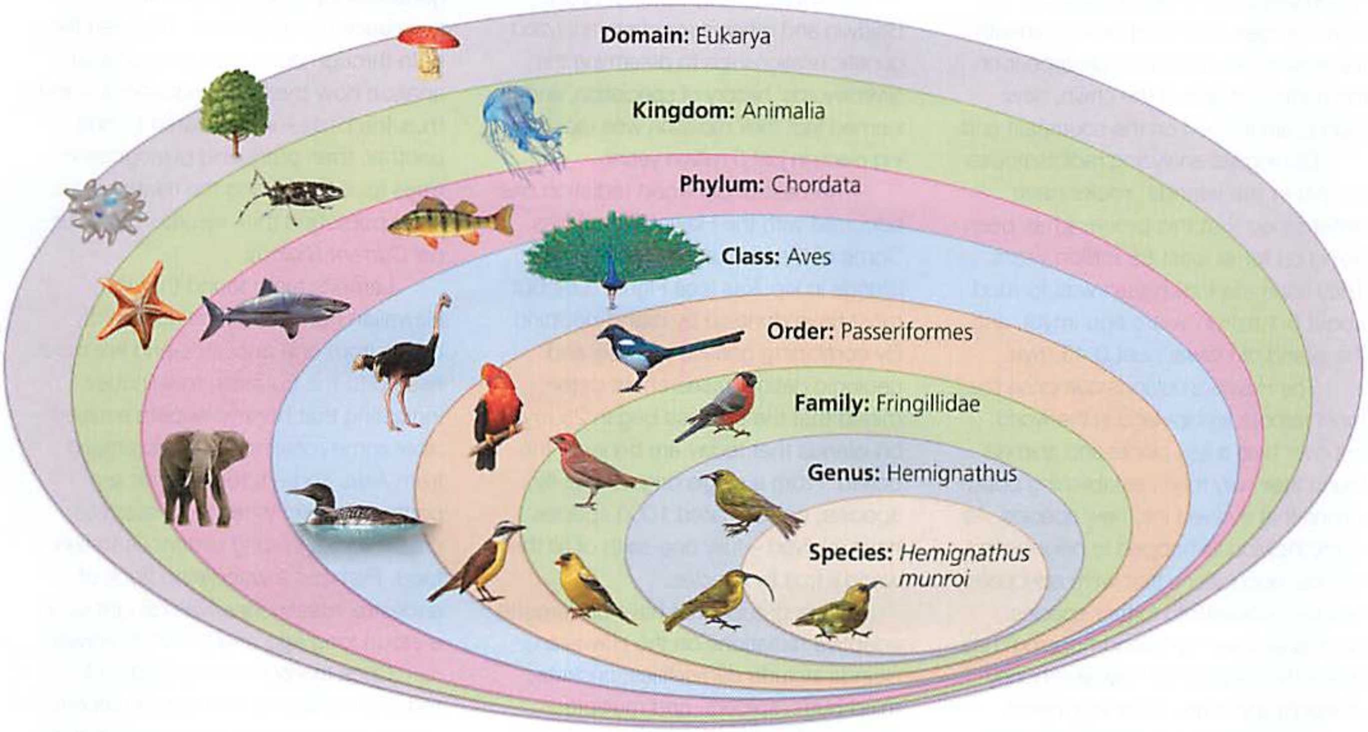


FIGURE 3.7 Taxonomists classify organisms using a hierarchical system meant to reflect evolutionary relationships. Species similar in appearance, behavior, and genetics (because they share recent common ancestry) are placed in the same genus. Organisms of similar genera are placed in the same family. Families are placed within orders, orders within classes, classes within phyla, phyla within kingdoms, and kingdoms within domains. For example, honeycreepers belong to the class Aves, along with peacocks, loons, and ostriches. However, the differences between these species, which have diverged across millions of years of evolution, are great enough that they are placed in different orders, families, and genera.

Hawaii: Species Factory and Lab of Evolution

For scientists who study how species form, no place on Earth is more fascinating and informative than the Hawaiian Islands, often called a "natural laboratory of evolution."

The key to this laboratory lies in the process that drives Hawaii's geologic history. Turn back to Figure 2.22 (Chapter 2, p. 41), and examine it closely. Deep beneath the Pacific Ocean, a volcanic "hotspot" spurts magma as the Pacific Plate slides across it in tectonic motion like a conveyor belt. Mountains of lava accumulate underwater until eventually a volcano rises above the waves, building an island. As the tectonic plate moves northwest, it carries each newly formed island with it, creating a long chain, or *archipelago*. Over several million years, each island gradually subsides, erodes, and disappears beneath the waves. As old islands disappear on the northwest end of the chain, new islands are formed on the southeast end.

Geologists analyzing radioisotopes (p. 24) in the islands' rocks have determined that this process has been going on for at least 85 million years. They estimate that Kaua'i was formed about 5.1 million years ago (mya), and the island of Hawai'i just 0.43 mya.

The Hawaiian Islands comprise the most remote archipelago in the world, but over time a few plants and animals found their way there, establishing populations that evolved into new species. As some individuals hopped to neighboring islands, populations that were adequately isolated evolved into further species. Such speciation by "island-hopping" has driven the radiation of Hawaiian honeycreepers and many other organisms.

For instance, the barren and windswept high volcanic slopes of Hawai'i are graced by some of the most striking flowering plants in the world, the silverswords (see Figure 3.1b). These spectacular plants have spiky, silvery leaves and tall stalks that explode into bloom with flowers once in the plant's long life before it dies. Researchers have discovered that Hawaii's 28 species of silverswords all evolved from a modest tarweed plant from California that reached Hawai'i and diversified by island-hopping. University of California–Berkeley botanist Bruce Baldwin and other researchers analyzed genetic relationships to determine the silverswords' history of speciation, and learned that their radiation was rapid, taking place in just 5 million years.

Dr. Heather Lerner, of Earlham College

The best-understood radiation has occurred with the Hawaiian fruit flies. Some of these insects speciate within islands in kipukas (see Figure 3.5), but most have done so by island-hopping. By combining genetic analysis and geologic dating, researchers determined that the process began 25 mya on islands that today are beneath the ocean. From a single original fruit fly species, an estimated 1000 species have evolved—fully one-sixth of all the world's fruit fly species.

Other groups that have undergone adaptive radiations on the Hawaiian Islands include damselflies, crickets, mirid bugs, spiders, and multiple families of plants. Scientists propose that once a species colonizes an island, it can often spread and evolve rapidly because competitors are few and there tend to be unoccupied niches (p. 61).

The Hawaiian honeycreepers are so diverse that researchers have long puzzled over what type of bird gave rise to their radiation—and whether there was just one colonizing ancestor or many. In 2011, to clarify how the honeycreeper radiation took place, one research team combined genetic sequencing technology with resources from museum collections and our knowledge of Hawaiian geology.

Heather Lerner and five colleagues first took tissue samples from bird specimens in museum collections. Working with Robert Fleischer and Helen James at the Smithsonian Institution, Lerner, now at Earlham College in Indiana, sampled 19 species of honeycreepers plus 28 diverse types of finches from around the Pacific Rim that experts had identified as possible ancestors.

Lerner's team obtained data from 13 genes and from mitochondrial genomes by sequencing DNA (p. 29) from each tissue sample. They ran the data through computer programs to analyze how the DNA sequences—and thus the birds—were related to one another, then produced phylogenetic trees (p. 54) showing the relationships. They published their results in the journal *Current Biology*.

Lerner's team found that the Hawaiian honeycreepers apparently derive from one ancestor, and are most related to the Eurasian rosefinches, indicating that honeycreepers evolved after some rosefinch-like bird arrived from Asia. Today's rosefinches are partly nomadic; when food supplies crash, flocks fly long distances to find food. Perhaps a wandering flock of ancestral rosefinches was caught up in a storm long ago and blown to Hawai'i.

Once this common ancestor of today's rosefinches and honeycreepers arrived on an ancient Hawaiian island, its progeny adapted to conditions there by natural selection, resulting in modified bill shape, diet, and coloration. Every once in a great while, wandering birds colonized other islands, founding populations that each adapted to local conditions and might eventually evolve into separate species.

Because the age of each island is known, Lerner's team could calibrate rates of evolutionary change in the DNA sequences of the birds, and thus measure the age of each divergence. That is, they could tell how "old" each bird species is. They found that the rosefinch-like ancestor arrived by 5.7 mya, about the time that the oldest of today's main islands (Kaua'i and Ni'ihau) were forming. After O'ahu emerged 4.0–3.7 mya, the speciation process went into overdrive, giving rise to many new species with distinctively different colors, bill shapes, and habits. By the time Maui arose 2.4–1.9 mya, most of the major differences in body form and appearance had evolved (**FIGURE 1**).

Thus, most major innovations arose midway through the process, when O'ahu and Kaua'i were the main islands in the chain. After this burst of innovation, major changes were fewer, perhaps because most possibilities had been explored, or perhaps because the newer islands of Maui and Hawai'i were too close together to isolate populations adequately.

The team's data show that the age of each honeycreeper species does not neatly match the age of the island(s) it inhabits today. Instead, the island-hopping process was complex, with some birds hopping "backwards" from newer islands to older ones. Moreover, within each island there is great variation in climate, topography, and vegetation, as windward slopes catch moisture from trade winds over the ocean and become lush and green, whereas leeward slopes in the rainshadow (p. 100) are arid. The varied habitats and rugged topography create barriers that can lead to speciation within islands.

For all these reasons, the "natural laboratory" of Hawai'i still has much to teach us about how the honeycreepers and other groups have evolved, and how new species are formed. ■

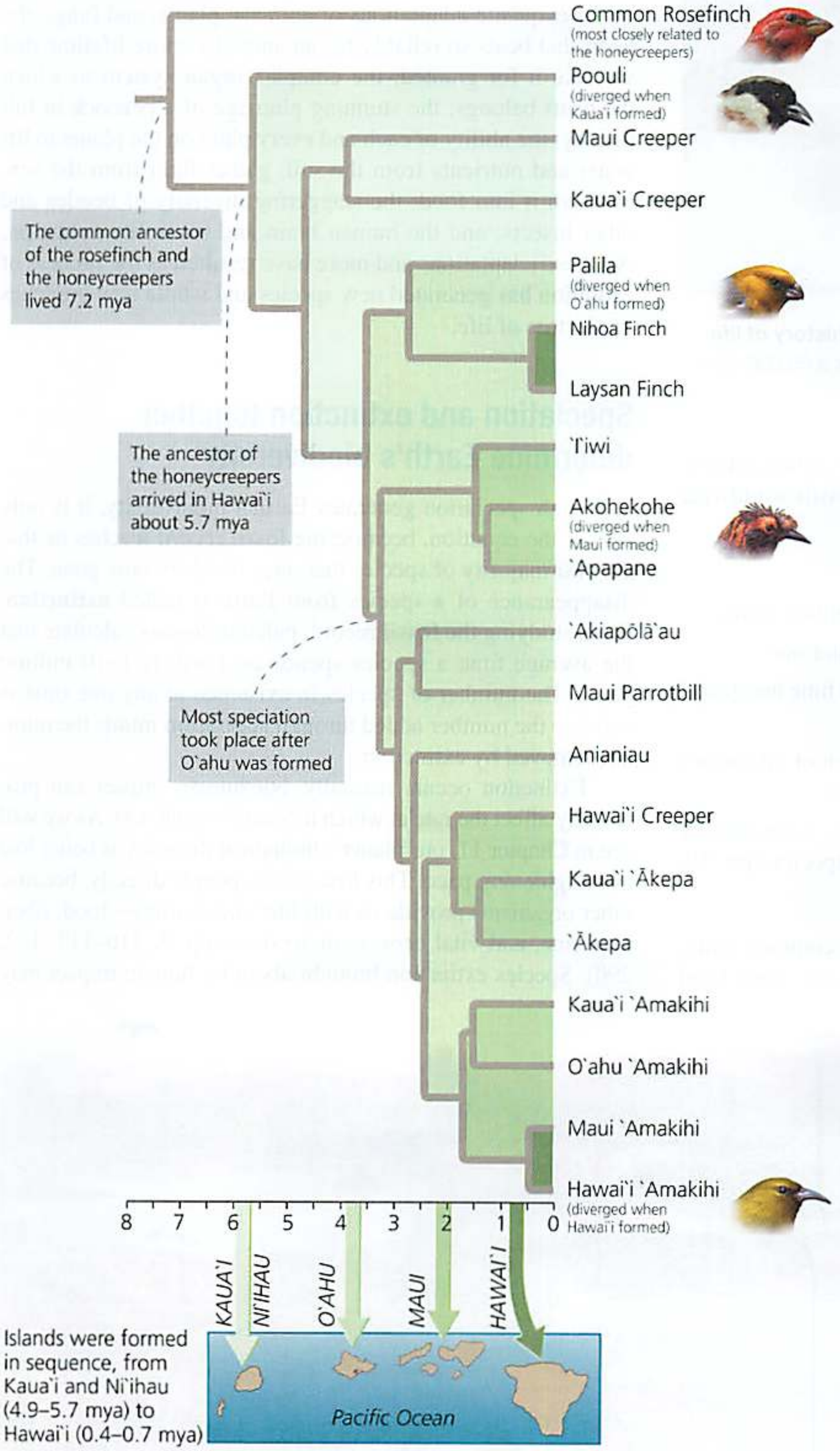


FIGURE 1 Using gene sequences, researchers generated this phylogenetic tree showing relationships among the Hawaiian honeycreepers. They then matched the history of the birds' diversification with the known geologic history of the islands' formation. *Adapted from: Lerner, H.R.L., et al. 2011. Multilocus resolution of phylogeny and timescale in the extant adaptive radiation of Hawaiian honeycreepers.* Curr Biol. *21: 1838–1844.*

FIGURE 3.8 The fossil record helps reveal the history of life on Earth. Here, a paleontologist in India excavates a 50,000-year-old fossilized elephant skull.

who study the history of Earth's life) can learn when particular organisms lived. The cumulative body of fossils worldwide is known as the **fossil record.**

The fossil record shows that:

- Life has existed on Earth for at least 3.5 billion years.
- Earlier types of organisms evolved into later ones.
- The number of species existing at any one time has generally increased through time.
- The species living today are a tiny fraction of all species that ever lived; the vast majority are extinct.
- There have been several episodes of *mass extinction*, or simultaneous loss of great numbers of species (pp. 59, 281–283).

Across life's 3.5 billion years on Earth, complex structures have evolved from simple ones, and large sizes from small ones. However, simplicity and small size have also evolved when favored by natural selection; it is easy to argue that Earth still belongs to the bacteria and other microbes, some of them little changed over eons.

Even fans of microbes, however, must marvel at some of the exquisite adaptations of animals, plants, and fungi: the heart that beats so reliably for an animal's entire lifetime that we take it for granted; the complex organ system to which the heart belongs; the stunning plumage of a peacock in full display; the ability of each and every plant on the planet to lift water and nutrients from the soil, gather light from the sun, and turn it into food; the staggering diversity of beetles and other insects; and the human brain and its ability to reason. All these adaptations and more have resulted as the process of evolution has generated new species and whole new branches on the tree of life.

Speciation and extinction together determine Earth's biodiversity

Although speciation generates Earth's biodiversity, it is only part of the equation, because the fossil record teaches us that the vast majority of species that once lived are now gone. The disappearance of a species from Earth is called **extinction.** From studying the fossil record, paleontologists calculate that the average time a species spends on Earth is 1–10 million years. The number of species in existence at any one time is equal to the number added through speciation minus the number removed by extinction.

Extinction occurs naturally, but human impact can profoundly affect the rate at which it occurs (**FIGURE 3.9**). As we will see in Chapter 11, our planet's biological diversity is being lost at a frightening pace. This loss affects people directly, because other organisms provide us with life's necessities—food, fiber, medicine, and vital ecosystem services (pp. 3, 116–117, 152, 290). Species extinction brought about by human impact may

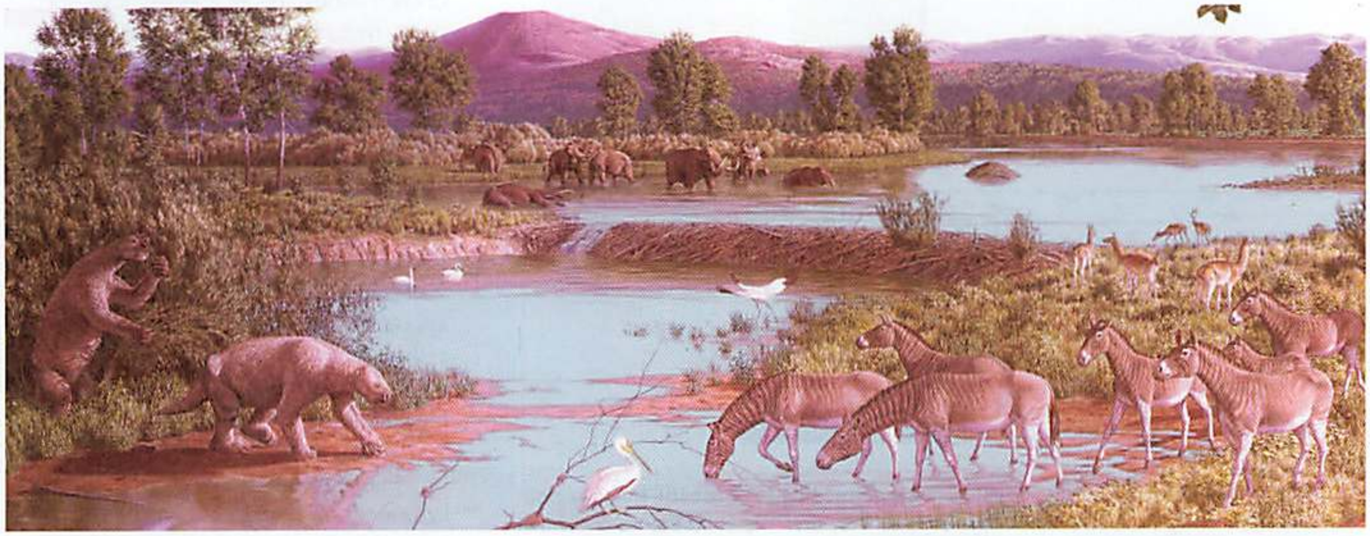


FIGURE 3.9 Until 10,000 years ago, the North American continent teemed with "megafauna"— mammoths, camels, giant ground sloths, lions, saber-toothed cats, and various types of horses, antelope, and bears. Nearly all these large mammals went extinct suddenly once people arrived on the continent. Similar extinctions occurred in other areas simultaneously with human arrival, suggesting to many scientists that overhunting or other human impacts were responsible. (See also Figure 11.8, p. 282.)

well be the single biggest problem we face, because the loss of a species is irreversible.

Some species are especially vulnerable to extinction

In general, extinction occurs when environmental conditions change rapidly or severely enough that a species cannot adapt genetically to the change; the slow process of natural selection simply does not have enough time to work. All manner of events can cause extinction—climate change, the arrival of new species, severe weather events, and more. In general, small populations are vulnerable to extinction because fluctuations in their size could, by chance, bring the population size to zero. Species narrowly specialized to some particular resource or way of life are also vulnerable, because environmental changes that make that resource or way of life unavailable can doom them. Species that are **endemic** to a region, meaning that they occur nowhere else on the planet, also face elevated risks of extinction because all their members belong to a single, sometimes small, population.

Island-dwelling species are frequently vulnerable. Because islands are smaller than mainland areas and are isolated by water, only some species reach islands, whereas many others never do. As a result, some of the pressures and challenges faced daily by organisms on the mainland simply don't exist on islands. For instance, only one land mammal—a bat—ever reached Hawai'i naturally, so Hawaii's birds evolved for millions of years without having to defend against the threat of predation by mammals. Likewise, Hawaii's plants did not need to protect themselves against plant-eating mammals. Because defenses are costly to invest in, most island birds and plants lost any defenses their ancestors may have had.

Eventually, people—first Polynesians and then Europeans—arrived in Hawai'i, bringing cattle, goats, pigs, rats, dogs, cats, and mongooses. Hawaii's native organisms were completely unprepared. Rats, cats, and mongooses preyed on ground-nesting seabirds, ducks, geese, an ibis, and flightless rails, driving a number of these birds extinct. Livestock ate through the vegetation, turning lush forests into desolate grasslands. All in all, half of Hawaii's native birds were driven extinct within just decades after human arrival.

On a mainland, "islands" of habitat (such as forested mountaintops) can host endemic species that are vulnerable to extinction (**FIGURE 3.10**). In the United States, many amphibians are limited to very small ranges. The Yosemite toad is restricted to a small region of the Sierra Nevada in California, the Houston toad occupies just a few areas of Texas woodland, and the Florida bog frog lives in a tiny region of Florida wetland. Fully 40 salamander species in the United States are restricted to areas the size of a typical county, and some of these live atop single mountains.

Earth has seen several episodes of mass extinction

Most extinction occurs gradually, one species at a time. The rate at which this type of extinction occurs is referred to as the *background extinction rate*. However, Earth has seen five events of staggering proportions that killed off massive numbers of species at once. These episodes, called **mass extinction events,** have occurred at widely spaced intervals in Earth's history and have wiped out 50–95% of our planet's species each time.

The best-known mass extinction occurred 65 million years ago and brought an end to the dinosaurs (although birds are modern representatives of dinosaurs). Evidence suggests that the impact of a gigantic asteroid caused this event, called the Cretaceous–Tertiary, or K–T, event. Still more catastrophic was the mass extinction at the end of the Permian period 250 million years ago (see **APPENDIX E** for Earth's geologic periods). Paleontologists estimate that 75–95% of all species may have perished during this event, described by one researcher as the "mother of all mass extinctions." Hypotheses as to what caused the end-Permian extinction event include an asteroid impact, massive volcanism, methane releases and global warming, or some combination of factors.

The sixth mass extinction is upon us

Many biologists have concluded that Earth is currently entering its sixth mass extinction event—and that we are the cause. Indeed, the Millennium Ecosystem Assessment (p. 15) estimated that today's extinction rate is 100–1000 times higher than the background rate, and rising (p. 283). Changes to Earth's natural systems set in motion by human population growth, development, and resource depletion have driven many species extinct and are threatening countless more. The alteration and outright destruction of natural habitats, the hunting and harvesting of species, and the introduction of species from one place to another where they can harm native

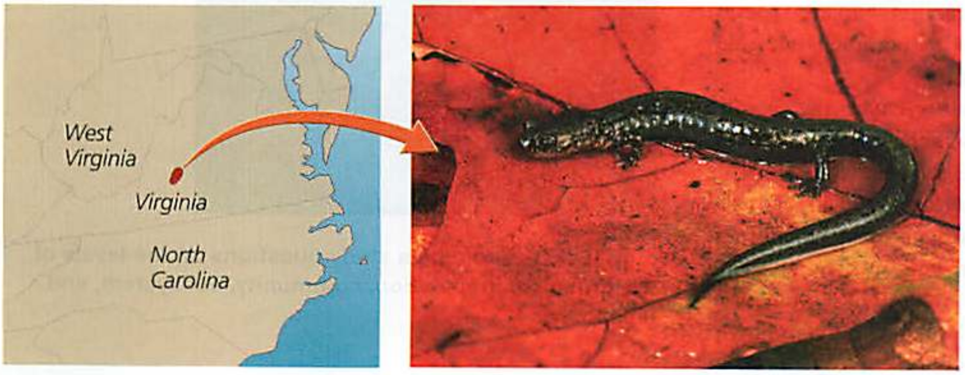


FIGURE 3.10 Small range sizes can leave species vulnerable to extinction if severe changes occur in their local environment. The Peaks of Otter salamander (*Plethodon hubrichti*) lives on only a few peaks in Virginia's Blue Ridge Mountains.

species—these processes and more have combined to threaten Earth's biodiversity (pp. 283–290).

When we look around us, it may not appear as though a human version of an asteroid impact is taking place, but we cannot judge such things on the timescale of a human lifetime. On the geologic timescale, extinction over 100 years or even 10,000 years appears instantaneous. In contrast, speciation is a slow enough process that it will take life millions of years to recover—by which time our own species will most likely not be around.

Levels of Ecological Organization

Extinction, speciation, and other evolutionary mechanisms and patterns play key roles in ecology. **Ecology** is the scientific study of the distribution and abundance of organisms, the interactions among organisms, and the relationships between organisms and their environments. It is often said that ecology provides the stage on which the play of evolution unfolds. The two are intertwined in many ways.

We study ecology at several levels

Life exists in a hierarchy of levels, from atoms, molecules, and cells (pp. 23–29) up through the **biosphere,** which is the cumulative total of living things on Earth and the areas they inhabit. Ecologists are scientists who study relationships at the higher levels of this hierarchy (FIGURE 3.11), namely at the levels of the organism, population, community, ecosystem, and biosphere.

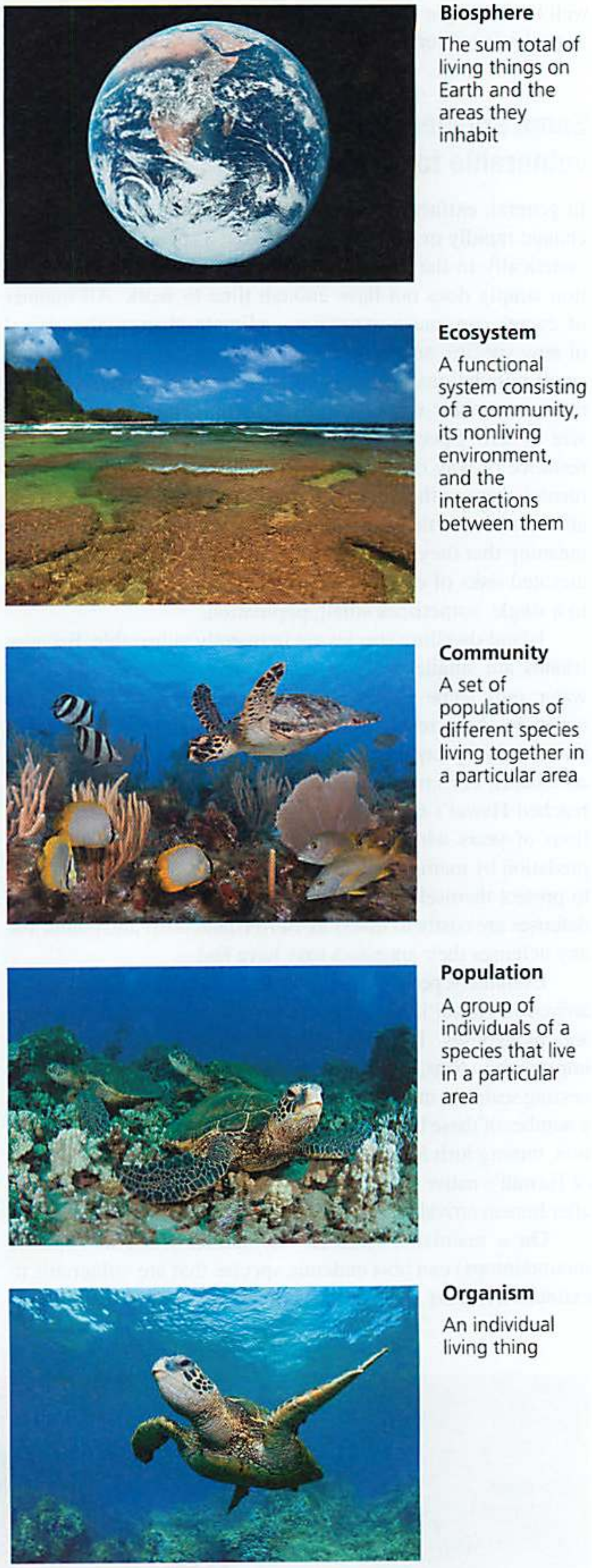


FIGURE 3.11 **Ecologists study questions on the levels of the organism, population, community, ecosystem, and biosphere.**

At the level of the organism, the science of ecology describes relationships between an organism and its physical environment. Organismal ecology helps us understand, for example, what aspects of a Hawaiian honeycreeper's environment are important to it, and why. In contrast, **population ecology** examines the dynamics of population change and the factors that affect the distribution and abundance of members of a population. It helps us understand why populations of some species (such as endangered honeycreepers) decline while populations of others (such as ourselves) increase.

In ecology, a **community** consists of an assemblage of populations of interacting species that live in the same area. A population of ʻakiapōlā ʻau, a population of koa trees, a population of wood-boring grubs, and a population of ferns, together with all the other interacting plant, animal, fungal, and microbial populations in the Hakalau Forest, would be considered a community. **Community ecology** focuses on patterns of species diversity and on interactions among species, ranging from one-to-one interactions to complex interrelationships involving the entire community.

Ecosystems encompass communities and the abiotic (nonliving) material and forces with which community members interact. Hakalau's cloud-forest ecosystem consists of its community plus the air, water, soil, nutrients, and energy used by the community's organisms. **Ecosystem ecology** reveals patterns, such as the flow of energy and nutrients, by studying living and nonliving components of systems in conjunction. Today's warming climate (Chapter 18) is having ecosystem-level consequences as it exerts impacts on the organisms of

Hakalau and many other ecosystems throughout the world. As new technologies allow scientists to learn more about the complex dynamics of natural systems at a global scale, ecologists are increasingly expanding their horizons beyond ecosystems to the biosphere as a whole.

In the remainder of this chapter we explore ecology up through the population level. In Chapter 4 we examine community ecology, and in Chapter 5 we consider ecology at the levels of the ecosystem and biosphere.

Each organism has habitat needs

At the level of the organism, each individual relates to its environment in ways that tend to maximize its survival and reproduction. One key relationship involves the specific environment in which an organism lives, its **habitat.** A species' habitat consists of the living and nonliving elements around it, including rock, soil, leaf litter, humidity, plant life, and more. The 'akiapōlā'au (**FIGURE 3.12**) lives in a habitat of cool, moist, montane forest of native koa and 'ōhi'a trees, where it is high enough in elevation to be safe from avian malaria.

Each organism thrives in certain habitats and not in others, leading to nonrandom patterns of **habitat use.** Mobile organisms actively select habitats in which to live from among the range of options they encounter, a process called **habitat selection.** In the case of plants and of rooted animals (such as sea anemones in the ocean), whose young disperse and settle passively, patterns of habitat use result from success in some habitats and failure in others.

Habitats are scale dependent. A tiny soil mite may use less than a square meter of soil in its lifetime. A vulture, elephant, or whale, in contrast, may traverse miles upon miles of air, land, or water in just a day. Species also may have different habitat needs in different seasons; many migratory birds use distinct breeding, wintering, and migratory habitats.

The criteria by which organisms favor some habitats over others can vary greatly. The soil mite may assess available habitats in terms of the chemistry, moisture, and texture of the soil and the percentage and type of organic matter. The vulture may ignore not only soil but also topography and vegetation, focusing solely on the abundance of dead animals in the area that it scavenges for food. For a whale, water temperature, salinity, and the density of marine microorganisms might be critical characteristics. Each species assesses habitats differently because each species has different needs.

FIGURE 3.12 The 'akiapōlā'au lives in a habitat of cool, moist, native forest on the slopes of Hawaiian volcanoes. It fills a unique niche by virtue of its odd bill, whose short, straight bottom half, and long, curved top half allows it to specialize on digging grubs out from native trees.

Habitat use is important in environmental science because the availability and quality of habitat are crucial to an organism's well-being. Indeed, because habitats provide everything an organism needs, including nutrition, shelter, breeding sites, and mates, the organism's very survival depends on the availability of suitable habitats. Often this need results in conflict with people who want to alter or develop a habitat for their own purposes.

Niche and specialization are key concepts in ecology

Another way in which an organism relates to its environment is through its niche. A species' **niche** reflects its use of resources and its functional role in a community. This includes its consumption of certain foods, its role in the flow of energy and matter, and its interactions with other organisms. The niche is a multidimensional concept, a kind of summary of everything an organism does. The pioneering ecologist Eugene Odum once wrote that "habitat is the organism's address, and the niche is its profession."

Organisms vary in the breadth of their niches. Species with narrow breadth, and thus very specific requirements, are said to be **specialists.** Those with broad tolerances, able to use a wide array of resources, are **generalists.** A native Hawaiian honeycreeper like the 'akiapōlā'au (see Figure 3.12) is a specialist, because its unique bill is exquisitely adapted for feeding on grubs that tunnel through the wood of native trees. In contrast, the common myna (a bird introduced to Hawai'i from Asia) is a generalist; its unremarkable bill allows it to eat many types of foods in many types of habitats. As a result, the common myna has spread through virtually all areas of the Hawaiian Islands where native birds have disappeared and where human development has altered the landscape. Today it is one of Hawaii's most numerous birds.

Specialists succeed over evolutionary time by being extremely good at the things they do, but they are vulnerable when conditions change and threaten the habitat or resource on which they have specialized. Generalists succeed by being able to live in many different places and to withstand variable conditions, but they may not thrive in any one situation as much as a specialist would. An organism's habitat preferences, niche, and degree of specialization each reflect adaptations of the species and are products of natural selection.

Population Ecology

Individuals of a species that inhabit a particular area make up a population. Species may consist of multiple populations that are geographically isolated from one another. This is the case with Hawaii's state bird, the nēnē, a goose that grazes in open grassy areas (see Figure 3.1d). Originally common throughout the Hawaiian Islands, the nēnē (pronounced "nay-nay") was nearly driven to extinction by human hunting; livestock and alien plants that destroyed and displaced the vegetation it fed on; and rats, cats, dogs, pigs, and mongooses that preyed on its eggs and young. Nēnēs disappeared from all islands except the island of Hawai'i, and in recent decades biologists and wildlife managers have labored to breed it in captivity and reintroduce it to protected areas on other islands. These efforts have met with success, and today nēnēs live in at least seven populations on four islands.

In contrast, the human species faces few threats from other animals, is a consummate generalist, and has spread into nearly every corner of the planet. As a result, it is difficult to define a distinct human population on anything less than the global scale. In the ecological sense of the word, all 7 billion of us comprise one population.

Populations show characteristics that help predict their dynamics

All populations—from humans to nēnēs—exhibit characteristics that help population ecologists predict the future dynamics of the population. Attributes such as density, distribution, sex ratio, age structure, and birth and death rates all help the ecologist understand how a population may grow or decline. The ability to predict growth or decline is useful in monitoring and managing threatened and endangered species (see **THE SCIENCE BEHIND THE STORY**, pp. 64–65). It is also useful in studying human populations (Chapter 8). Understanding human population dynamics is a central element of environmental science and is one of the prime challenges for our society today.

Population size Expressed as the number of individual organisms present at a given time, **population size** may increase, decrease, undergo cyclical change, or remain stable over time. Populations generally grow when resources are abundant and natural enemies are few. Populations can decline in response to loss of resources, negative impacts from other species, or natural disasters that kill large numbers of individuals. Researchers estimate that the nēnē population surpassed 25,000 birds before Europeans reached the Hawaiian Islands. By the 1950s, after two centuries of impacts from hunting, agriculture, non-native mammals, and invasive plants, the population was down to just 30 individuals. Since then, intensive conservation efforts have turned this decline around, and now over 2000 nēnēs live on the Hawaiian Islands.

The passenger pigeon, now extinct, illustrates the extremes of population size (**FIGURE 3.13**). Not long ago it was the most abundant bird in North America; flocks of passenger pigeons literally darkened the skies. In the early 1800s, ornithologist Alexander Wilson watched a flock of 2 billion birds 390 km (240 mi) long that took 5 hours to fly over and sounded like a tornado. Passenger pigeons nested in gigantic colonies in the forests of the upper Midwest and southern Canada. Once settlers arrived and began cutting the forests, however, the birds made easy targets for market hunters, who gunned down thousands at a time and shipped them to market by the wagonload. By the end of the 19th century, the passenger pigeon population had declined to such a low number that the birds could not form the large colonies they apparently needed in order to breed. In 1914, the last passenger pigeon on Earth died in the Cincinnati Zoo, bringing the continent's most numerous bird species to extinction within just a few decades.

Population density The flocks and breeding colonies of passenger pigeons showed high population density, another attribute that ecologists assess to understand populations. **Population density** describes the number of individuals in a population per unit area. High population density makes it easier for organisms to group together and find mates, but it can

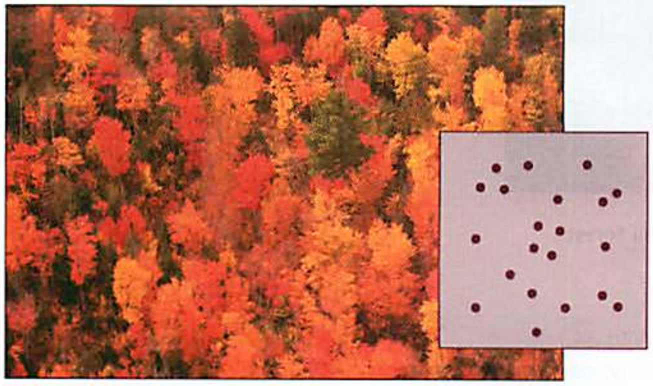
(a) Passenger pigeon

(b) 19th-century lithograph of pigeon hunting in Iowa

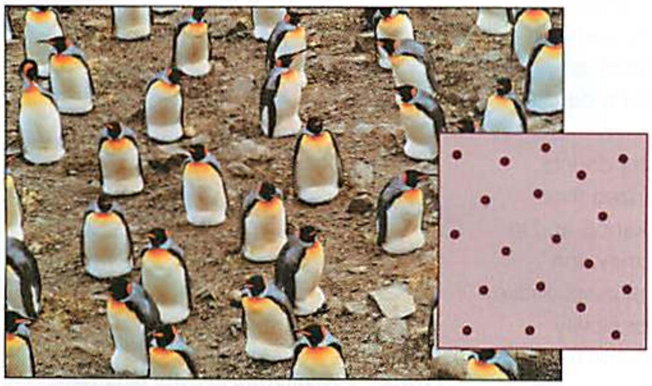
FIGURE 3.13 The passenger pigeon was once North America's most numerous bird. Its flocks literally darkened the skies when millions of birds passed overhead. However, hunting and deforestation drove the species to extinction within just a few decades.

also lead to competition and conflict if space, food, or mates are in limited supply. Overcrowded organisms may become vulnerable to the predators that feed on them, and close contact among individuals can increase the transmission of infectious disease. For these reasons, organisms sometimes leave an area when densities become too high. In contrast, at low population densities, organisms benefit from more space and resources but may find it harder to locate mates and companions.

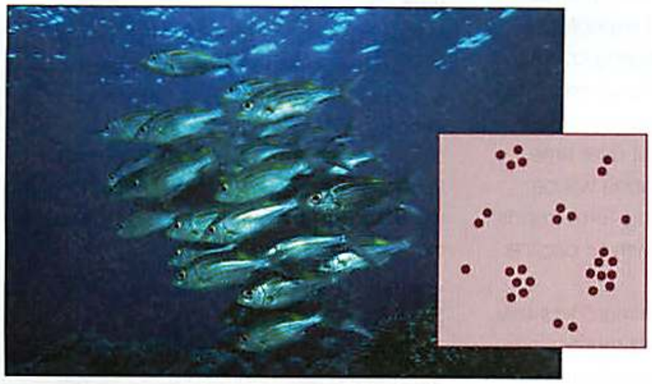
Population distribution **Population distribution** describes the spatial arrangement of organisms in an area. Ecologists define three distribution types: random, uniform, and clumped (FIGURE 3.14). In a *random distribution*, individuals are located haphazardly in no particular pattern. This type of distribution can occur when the resources an organism needs are plentiful throughout an area and other organisms do not strongly influence where members of a population settle.



(a) Random: Distribution of organisms displays no pattern.



(b) Uniform: Individuals are spaced evenly.



(c) Clumped: Individuals concentrate in certain areas.

FIGURE 3.14 Individuals in a population can spatially distribute themselves in three fundamental ways.

A *uniform distribution* is one in which individuals are evenly spaced. This can occur when individuals hold territories or compete for space. In a desert where water is scarce, each plant needs space for its roots to gather moisture. Plants may even poison one another's roots as a means of competing for space. As a result, plants may end up growing at equal distances from one another.

In a *clumped distribution*, the pattern most common in nature, organisms arrange themselves according to the availability of the resources they need to survive. Many Hawaiian honeycreepers tend to cluster near actively flowering trees that offer nectar. Many desert plants grow in patches around isolated springs or along streambeds that flow with water after rains. Human beings also exhibit clumped distribution: People frequently aggregate in villages, towns, or cities. Clumped distributions often indicate that species are seeking certain habitats or resources that are themselves clumped.

Distributions can depend on the scale at which one measures them. At small scales a population may be distributed uniformly, yet this may occur within one patch of a larger, clumped distribution. At very large scales, all organisms show clumped or patchy distributions, because some parts of the total area they inhabit are bound to be more hospitable than others.

Sex ratio A population's **sex ratio** is its proportion of males to females, and this can influence whether the population will increase or decrease in size over time. In monogamous species (in which each sex takes a single mate), a 1:1 sex ratio maximizes population growth, whereas an unbalanced ratio leaves many individuals of one sex without mates. Most species are not monogamous, however, so sex ratios may vary from one species to another.

Age structure Populations generally consist of individuals of different ages. **Age distribution,** or **age structure,** describes the relative numbers of organisms of each age within a population. By combining this information with data on the reproductive potential of individuals in each age class, a population ecologist can predict how the population may grow or shrink.

For many plants and animals that continue growing in size as they age, older individuals reproduce more: A tree that is large because it is old can produce more seeds, and a fish that is large because it is old may produce more eggs. In some animals, such as birds, the experience they gain with age often makes older individuals better breeders.

Human beings are unusual because we often survive past our reproductive years. A human population made up largely of older (post-reproductive) individuals will tend to decline over time, whereas one with many young people (of reproductive or pre-reproductive age) will tend to increase. We will use diagrams to explore these ideas further in Chapter 8 (pp. 197–199) as we study human population growth.

THE SCIENCE BEHIND THE STORY

Monitoring Bird Populations at Hakalau Forest

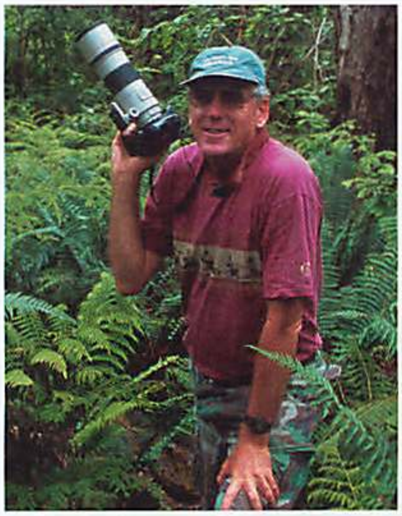
Are populations of honeycreepers increasing or decreasing? It's a high-stakes question. The answer could tell us whether management efforts to save them are on the right track, or whether the birds may be headed for extinction.

At Hakalau Forest National Wildlife Refuge, on the rainy slope of Mauna Kea on the island of Hawai‘i, biologists have been working hard for years to understand the dynamics of bird populations. But monitoring population trends is not easy, and there is still debate and uncertainty.

Established in 1985, the Hakalau Refuge is home to nine species of native forest birds, including four federally endangered ones: the Hawai‘i ‘ākepa, the Hawai‘i creeper, the ‘akiapōlā‘au, and the ‘io, or Hawaiian hawk. A number of non-native birds now occur here as well. Much of the region's native forest had been cleared for cattle ranching years ago, while free-roaming pigs and invasive plants had degraded the rest.

The biologists employed after 1985 to manage Hakalau fenced pigs and feral cattle out of the forest and labored to restore the area by removing invasive weeds and by raising and planting half a million native plants. Gradually the damaged forest recovered, and stands of young trees took root at higher elevations. But has the restored forest brought higher populations of native forest birds?

Beginning in 1987, federal biologists and trained observers conducted regular surveys of birds on the refuge. Following protocols commonly used by field ornithologists, they performed "point counts" by walking transects and stopping for 8 minutes at a time in predetermined spots and counting numbers of each species seen or heard. With 343 points along 15 transects across the refuge, this sampling allowed them to estimate population densities for each bird species. Researchers then analyzed changes in these samples through time to make inferences about changes in population densities and population sizes.



Jack Jeffrey in the Hakalau Forest

After 21 years of point counts, refuge biologists summarized their analyses. At a 2008 workshop and in a 2009 technical report, they concluded that populations of most native birds were either stable or slowly increasing across most of the refuge.

Their report included a series of graphs similar to that shown in **FIGURE 1**. Densities of birds varied from year to year, which is normal and expected, as this may result from varying conditions (such as weather). Because of this variation, long-term studies are necessary; scientists expect that over time, random year-to-year variation will be overshadowed by true long-term trends that reveal the actual growth or decline of the population.

To interpret trends, researchers use a statistical method called *regression*. Linear regression mathematically analyzes how values change through time and determines a straight line that can be drawn through them to most accurately represent their trend. Linear regression thus places a "line of best fit" through the data points on a graph (see Figure 1).

With the data from Hakalau, linear regression led managers to conclude that over the 21-year period:

- In high-elevation pasture that managers were restoring to forest, populations of birds that used the young trees were rising sharply.
- In middle-elevation open forest being managed, populations of all native birds were either stable or increasing.

The long-term picture thus appeared bright.

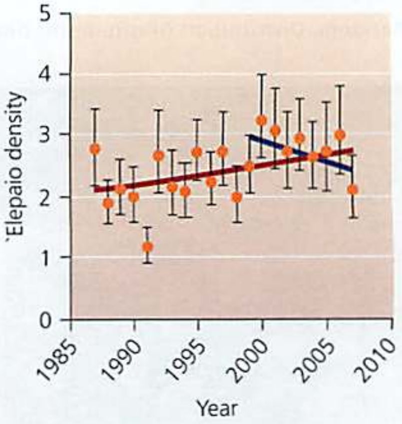


FIGURE 1 Population density data for the Hawai‘i ‘elepaio, a native forest bird, typify data gathered at Hakalau Forest NWR. Over a 21-year period, regression shows an increase (red line), yet over the most recent 9 years, regression shows a decrease (blue line). Thin black bars indicate 95% confidence intervals. *Data from Camp, Richard J., et al. 2009.* Passerine bird trends at Hakalau Forest National Wildlife Refuge, Hawai‘i. *Hawai‘i Cooperative Studies Unit Technical Report HCSU-011.*

DATA Q What is the trend in the data during the first 12 years of the period shown? Can you draw a line through the first 12 data points that you feel best represents this trend?

However, during the most recent 9 years of the 21-year period, many of the populations had decreased. Regressions run on the last 9 years alone showed apparent declines for many species (see Figure 1).

Biologist Leonard Freed of the University of Hawai'i at Manoa argued that federal biologists were overemphasizing the positive long-term trends and ignoring the negative near-term trends. For years, Freed and his colleagues had conducted research within Hakalau, focusing on the breeding biology of the Hawai'i 'ākepa (**FIGURE 2a**). Their research suggested that the 'ākepa began suffering competition for food once the non-native Japanese white-eye (**FIGURE 2b**) became abundant in the forest. This competition, along with attacks from parasitic lice in the nest, stunted the growth of young birds, Freed maintained, and threatened the 'ākepa population. Freed urged that white-eyes be trapped and killed in order to save the 'ākepa. Refuge biologists called Freed's results controversial and said they needed validation.

The debate came to a head in a pair of papers published back-to-back in the ornithological journal *Condor* in 2010. The team of federal biologists, led by Richard Camp and including Jack Jeffrey, presented their data and acknowledged that many populations showed downward trends in the most recent 9 years. Freed and his colleague Rebecca Cann reanalyzed the federal data using alternative methods and questioned whether the earlier apparent increases were reliable.

At stake is how to manage the forest and its birds. If Camp and his colleagues are right, then management actions taken so far seem to have been effective, boosting populations or holding them stable in the face of dire threats. If Freed and Cann are right, then management strategies may need to be rethought. Researchers on all sides are debating the issues diligently because they care deeply about the forest and its birds and are trying their utmost to save them during a time of crisis.

Many factors could account for the apparent recent declines in populations of 'ākepas and other native honeycreepers, including the simple fact that thicker forest vegetation has made it harder for counters to detect birds. Of concern, though, is the possibility that challenges from outside the refuge—such as malaria and pox being driven upslope by climate warming—might eventually overwhelm even the best management efforts.

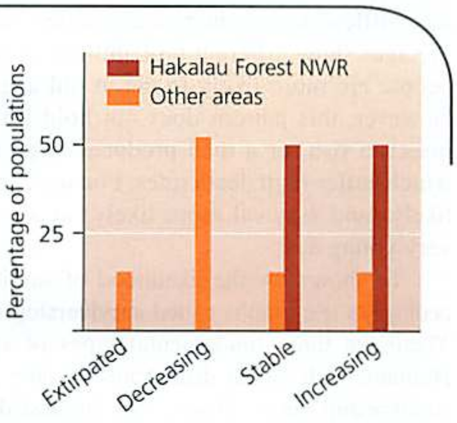


FIGURE 3 At Hakalau Forest NWR, native forest bird populations were judged to be stable or increasing, whereas at four other protected areas on the island of Hawai'i, most populations were judged to be decreasing, and some have recently vanished. *Data from Camp, Richard J., et al. 2009.* Passerine bird trends at Hakalau Forest National Wildlife Refuge, Hawai'i. *Hawai'i Cooperative Studies Unit Technical Report HCSU-011.*

Today researchers continue to survey Hakalau's birds, adding to their valuable long-term database of population trends. But government budget cuts are threatening their ability to analyze the data, as well as their capacity to safeguard the refuge. Amid cuts in funding and staffing, pigs broke through fences and began degrading the newly restored forest. Most funding was recently reinstated, but each time budget cuts are made, refuge staff must work hard at greater expense just to regain the progress previously made.

Despite the apparent recent declines in bird populations at Hakalau, populations there seem to be faring better than elsewhere on the island of Hawai'i (**FIGURE 3**). Moreover, the reforestation of Hakalau's upper zone is creating new habitat into which birds are moving. This success is a hopeful sign that research and careful management can help undo past damage and preserve endangered island species. ●

(a) Hawai'i 'ākepa

(b) Japanese white-eye

FIGURE 2 Work by biologist Leonard Freed suggests that the 'ākepa is suffering competition from the non-native Japanese white-eye.

Birth and death rates All the preceding factors can influence the rates at which individuals within a population are born and die. Just as individuals of differing ages have different reproductive capacities, individuals of differing ages show different probabilities of dying. For instance, people are more likely to die at old ages than young ages. However, this pattern does not hold for all organisms. An insect, a fish, or a toad produces large numbers of young, which suffer high death rates. For such animals, death is less likely (and survival more likely) at an older age than at a very young age.

To show how the likelihood of survival varies with age, ecologists use graphs called **survivorship curves** (**FIGURE 3.15**). There are three fundamental types of survivorship curves. Humans, with higher death rates at older ages, show a type I survivorship curve. Toads, with highest death rates at young ages, show a type III survivorship curve. A type II survivorship curve is intermediate and indicates equal rates of death at all ages. Many birds are thought to show type II curves.

Populations may grow, shrink, or remain stable

Now that we have outlined some key attributes of populations, we are ready to take a quantitative view of population change by examining some simple mathematical concepts used by population ecologists and by **demographers** (scientists who study human populations). Population growth, or decline, is determined by four factors:

- Births within the population (*natality*)
- Deaths within the population (*mortality*)
- **Immigration** (arrival of individuals from outside the population)
- **Emigration** (departure of individuals from the population)

Births and immigration add individuals to a population, whereas deaths and emigration remove individuals. A convenient way to express rates of birth and death is to measure the number of births and deaths per 1000 individuals per year. These rates are termed the *crude birth rate* and the *crude death rate*.

If we are not interested in the effects of migration, we can measure the **rate of natural increase** by subtracting the crude death rate from the crude birth rate:

$$\text{(crude birth rate)} - \text{(crude death rate)} = \text{rate of natural increase}$$

The rate of natural increase reflects the degree to which a population is growing or shrinking as a result of its own internal factors.

To obtain an overall **population growth rate,** the total rate of change in a population's size per unit time, we must also take into account the effects of migration. Thus, we include terms for immigration and emigration (each expressed per 1000 individuals per year) in the formula, as follows:

$$\text{(crude birth rate} - \text{crude death rate)} + \text{(immigration rate} - \text{emigration rate)} = \text{population growth rate}$$

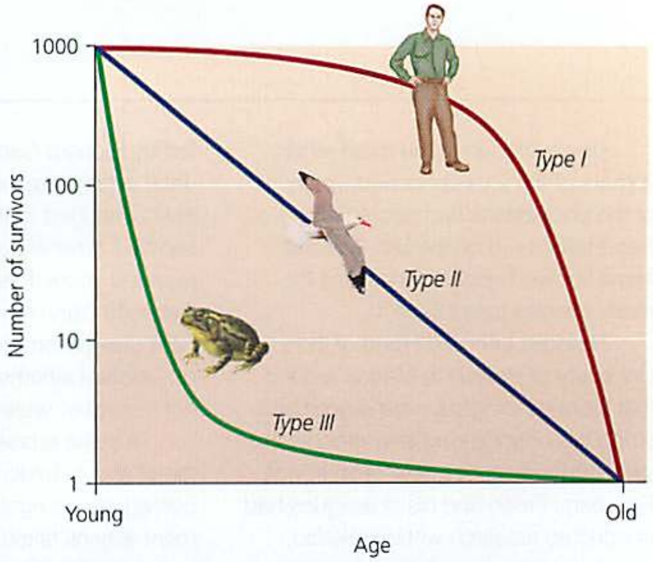


FIGURE 3.15 Survivorship curves show how an individual's likelihood of survival varies with age. In a type I survivorship curve, survival rates are high when organisms are young and decrease sharply when organisms are old. In a type II survivorship curve, survival rates are equivalent regardless of an organism's age. In a type III survivorship curve, most mortality takes place at young ages, and survival rates are greater at older ages.

DATA Q Which organism has the highest rate of survival at a young age: a toad, a bird, or a human being?

The resulting number tells us the net change in a population's size per 1000 individuals per year. For example, a population with a crude birth rate of 18 per 1000/yr, a crude death rate of 10 per 1000/yr, an immigration rate of 5 per 1000/yr, and an emigration rate of 7 per 1000/yr would have a population growth rate of 6 per 1000/yr:

$$(18/1000 - 10/1000) + (5/1000 - 7/1000) = 6/1000$$

Thus, a population of 1000 in one year will reach 1006 in the next. If the population is 1,000,000, it will reach 1,006,000 the next year. Such population increases are often expressed as percentages, which we can calculate using the following formula:

$$\text{population growth rate} \times 100\%$$

Thus, a growth rate of 6/1000 would be expressed as:

$$6/1000 \times 100\% = 0.6\%$$

By measuring population growth in terms of percentages, scientists can compare increases and decreases in species that have far different population sizes. They can also project changes that will occur in the population over longer periods, much like you might calculate the amount of interest your savings account will earn over time.

Unregulated populations increase by exponential growth

When a population increases by a fixed percentage each year, it is said to undergo **exponential growth.** Imagine you put money in a savings account at a fixed interest rate and leave it untouched for years. As the principal accrues interest and grows larger, you earn still more interest, and the sum grows by escalating amounts each year. The reason is that a fixed percentage of a small number makes for a small increase, but the same percentage of a large number produces a large increase. Thus, as savings accounts (or populations) become larger, each incremental increase likewise gets larger. Such acceleration is a characteristic of exponential growth.

We can visualize changes in population size by using population growth curves. The J-shaped curve in **FIGURE 3.16** shows exponential growth. Populations of organisms increase exponentially unless they meet constraints. Each organism reproduces by a certain amount, and as populations get larger, there are more individuals reproducing by that amount. If there are adequate resources and no external limits, ecologists theoretically expect exponential growth.

Normally, exponential growth occurs in nature only when a population is small, competition is minimal, and environmental conditions are ideal for the organism in question. Most often, these conditions occur when the organism is introduced to a new environment that contains abundant resources to exploit. Mold growing on a piece of fruit, or bacteria colonizing a recently dead animal, are cases in point. Plants colonizing regions during primary succession (p. 85) after glaciers recede or volcanoes erupt may also grow exponentially. In Hawai'i, many of the species that colonized the islands from other locations underwent exponential growth for a time after their arrival. One current example of exponential growth in the mainland United States is the Eurasian collared dove (see Figure 3.16). Unlike its extinct relative the passenger pigeon, this species arrived here from Europe, thrives in human-disturbed areas, and has spread across North America in a matter of years.

Limiting factors restrain population growth

Exponential growth rarely lasts long. If even a single species were to increase exponentially for very many generations, it would blanket the planet's surface! Instead, every population eventually is constrained by **limiting factors**—physical, chemical, and biological attributes of the environment that restrain population growth. These limiting factors determine the **carrying capacity,** the maximum population size of a species that a given environment can sustain.

Ecologists use the S-shaped curve in **FIGURE 3.17** to show how an initial exponential increase is slowed and eventually brought to a standstill by limiting factors. Called the **logistic growth curve,** it rises sharply at first but then begins to level off as the effects of limiting factors become stronger. Eventually the collective force of these factors stabilizes the population size at its carrying capacity.

We can witness this process by taking a closer look at the data for the Eurasian collared dove population, as gathered by thousands of volunteer birders and analyzed by government biologists through the Breeding Bird Survey, a long-running citizen science project. The dove first reached North America in Florida a few decades ago and subsequently spread north and west. Today its numbers are growing fastest in western areas it has recently reached, and slower in eastern areas where it has been present for longer. In Florida, it has apparently reached carrying capacity (**FIGURE 3.18**). Populations of other European birds that spread across North America in the past, such as the house sparrow and European starling, have peaked and are today beginning to decline.

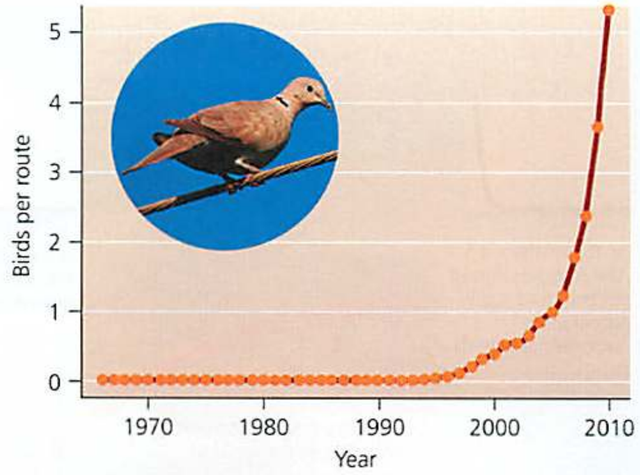


FIGURE 3.16 A population may grow exponentially for a time when colonizing an unoccupied environment or exploiting an unused resource. The Eurasian collared dove is currently spreading across the North American continent, propelled by exponential growth. *Data from Sauer, J.R., et al., 2011.* The North American Breeding Bird Survey, results and analysis 1966–2009. *v. 3.23.2011. USGS Patuxent Wildlife Research Center, Laurel, MD.*

Many factors influence a population's growth rate and carrying capacity. For animals in terrestrial environments, limiting factors include temperature extremes; prevalence of disease; abundance of predators; and the availability of food, water, mates, shelter, and suitable breeding sites. Plants are often limited by amounts of sunlight and moisture and the type of soil chemistry, in addition to disease and attack from plant-eating animals. In aquatic systems, limiting factors include salinity, sunlight, temperature, dissolved oxygen, fertilizers, and pollutants. To determine limiting factors, ecologists may conduct

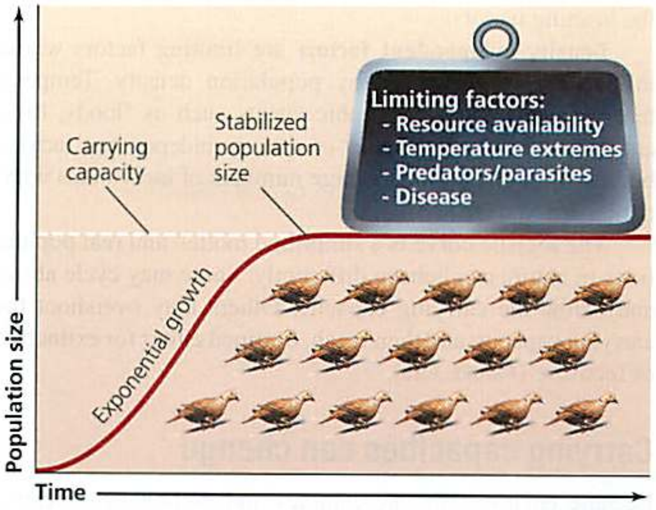


FIGURE 3.17 The logistic growth curve shows how population size may increase rapidly at first, then grow more slowly, and finally stabilize at a carrying capacity. Carrying capacity is determined both by the *biotic potential* of the organism and by various external limiting factors.

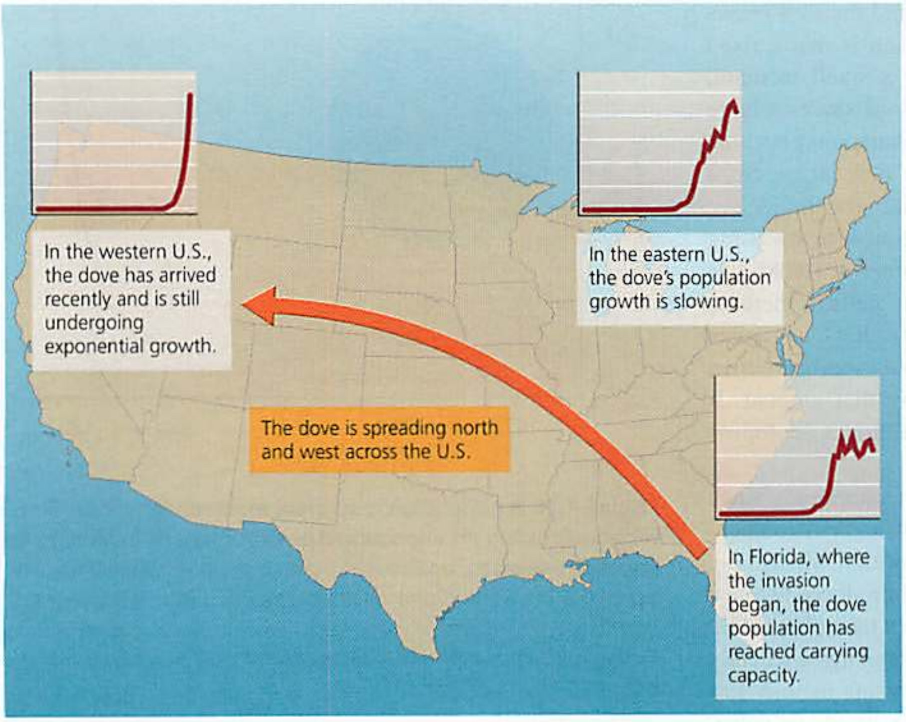


FIGURE 3.18 Exponential growth slows down over time and gives way to logistic growth. By breaking down the continent-wide data for the Eurasian collared dove from Figure 3.16, we can track its spread to the north and west of Florida, where it first arrived. Today its population growth is fastest in the west, slower in the east (where the species has been present for longer), and stable in Florida (where it has apparently reached carrying capacity). *Data from Sauer, J.R., et al., 2011.* The North American Breeding Bird Survey, results and analysis 1966–2009. *v. 3.23.2011. USGS Patuxent Wildlife Research Center, Laurel, MD.*

DATA Q Looking ahead several decades into the future, what do you predict the population growth graph for the western United States will look like?

experiments in which they increase or decrease a hypothesized limiting factor and observe its effects on population size.

The influence of some factors depends on population density

A population's density can enhance or diminish the impact of certain limiting factors. Recall that high population density can help organisms find mates but can also increase competition and the risk of predation and disease. Such factors are said to be **density-dependent factors,** because their influence rises and falls with population density. The logistic growth curve in Figure 3.17 represents the effects of density dependence. The larger the population size, the stronger the effects of the limiting factors.

Density-independent factors are limiting factors whose influence is not affected by population density. Temperature extremes and catastrophic events such as floods, fires, and landslides are examples of density-independent factors, because they can eliminate large numbers of individuals without regard to their density.

The logistic curve is a simplified model, and real populations in nature can behave differently. Some may cycle above and below the carrying capacity. Others may overshoot the carrying capacity and then crash, destined either for extinction or recovery (**FIGURE 3.19**).

Carrying capacities can change

Because environments are complex and ever-changing, carrying capacity can vary. If a fire destroys a forest, for example, the carrying capacities for most forest animals will decline, whereas carrying capacities for species that benefit from fire will increase. Our own species has proved capable of intentionally altering our environment so as to raise our carrying capacity. When our ancestors began to build shelters and use fire for heating and cooking, they eased the limiting factors of cold climates and were able to expand into new territory. As human civilization has developed, we have overcome limiting factors time and again through the development of new technologies and cultural institutions. People have managed so far to increase the planet's carrying capacity for our species, but we have done so by appropriating immense proportions of the planet's resources. In the process, we have reduced carrying capacities for countless other organisms that rely on those same resources.

WEIGHING THE ISSUES

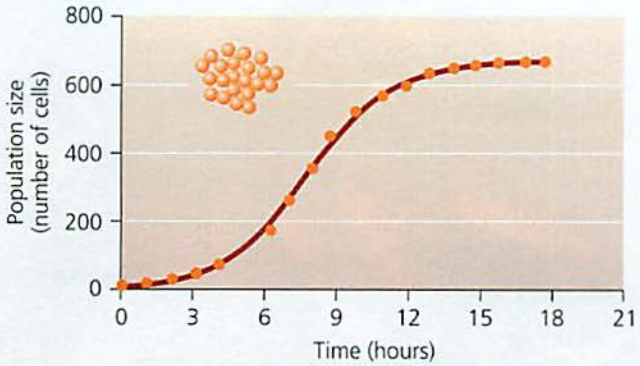
CARRYING CAPACITY AND HUMAN POPULATION GROWTH

The global human population has passed 7 billion, and we have far exceeded our planet's historic carrying capacity for people. Name some specific means by which you think we have accomplished this. What limiting factors exist for the human population today? Do you think we can continue to raise our carrying capacity? Might Earth's future carrying capacity for us decrease? Why or why not?

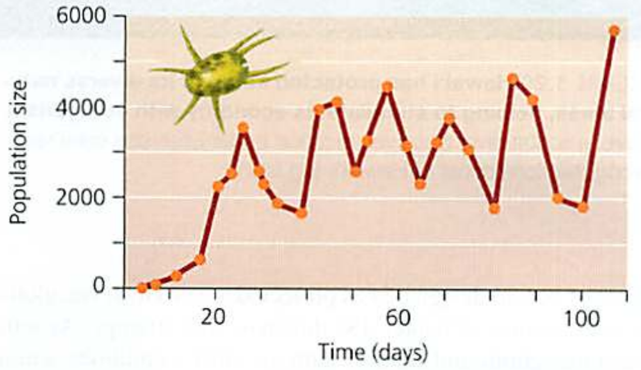
Reproductive strategies vary among species

Limiting factors from an organism's environment help to regulate its population size, but the attributes of the organism also matter. For example, organisms differ in their *biotic potential*, or capacity to produce offspring. A fish with a short gestation period that lays thousands of eggs at a time has high biotic potential, whereas a whale with a long gestation period that gives birth to a single calf at a time has low biotic potential.

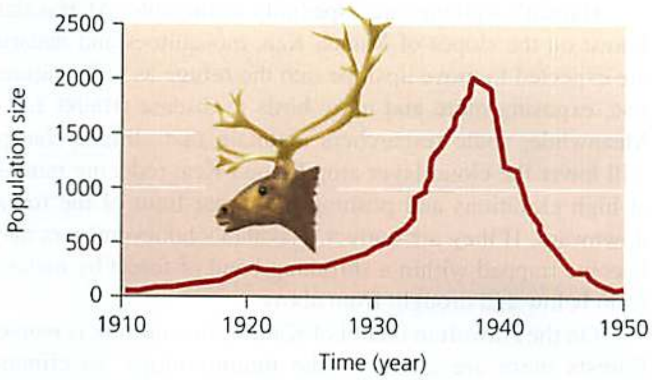
Giraffes, elephants, humans, and other large animals with low biotic potential produce relatively few offspring during their lifetimes. Species that take this approach to reproduction



(a) Yeast cells, *Saccharomyces cerevisiae*



(b) Mite, *Eotetranychus sexmaculatus*



(c) St. Paul reindeer, *Rangifer tarandus*

FIGURE 3.19 Population growth in nature may depart from the logistic growth curve in various ways. Yeast cells from an early lab experiment show logistic growth **(a)** that closely matches the theoretical model. Some organisms, such as the mite shown here, show cycles **(b)** in which population fluctuates above and below the carrying capacity. Populations that rise too fast and deplete resources may crash just as suddenly **(c)**, such as the population of reindeer introduced to the Bering Sea island of St. Paul. *Data from: (a) Pearl, R., 1927. The growth of populations.* Quarterly Review of Biology *2: 532–548; (b) Huffaker, C.B., 1958. Experimental studies on predation: Dispersion factors and predator-prey oscillations.* Hilgardia *27: 343–383, Figure 7, © 1958 by the Regents of the University of California; (c) Adapted from Scheffer, Victor B., 1951. The rise and fall of a reindeer herd.* The Scientific Monthly *73: 356–362, Fig. 1. Reprinted with permission from AAAS.*

require a long time to gestate and raise their young, but the considerable energy and resources they devote to caring for and protecting them helps give these few offspring a high likelihood of survival. Such species are said to be **K-selected** (because their populations tend to stabilize over time near carrying capacity, commonly abbreviated *K*). Because their populations stay close to carrying capacity, these organisms must compete to hold their own in a crowded world. Thus, natural selection favors investing in high-quality offspring that can be good competitors.

In contrast, species that are **r-selected** have high biotic potential and devote their energy and resources to producing many offspring in a short time. Their offspring do not require parental care after birth, so r-strategists simply leave their survival to chance. The abbreviation *r* denotes the per capita rate at which a population increases in the absence of limiting factors. Population sizes of r-selected species fluctuate greatly, such that they are often well below carrying capacity. This is why natural selection in these species favors traits that lead to rapid population growth. Many fish, plants, frogs, insects, and others are r-selected.

It is important to note, however, that *these are two extremes on a continuum* and that most species fall somewhere between the extremes of r-selected and K-selected species. Moreover, many organisms show combinations of traits that do not correspond to a place on the continuum. A redwood tree, for instance, is large and long-lived, yet it produces many small seeds and offers no parental care.

Conserving Biodiversity

Environmental changes that affect populations have been taking place as long as life has existed, but today human development, resource extraction, and population pressure are speeding the rate of change and altering the types of change. Science is crucial in helping us understand how we modify our environment. However, the threats to biodiversity have complex social, economic, and political roots, so environmental scientists recognize that we must also understand these aspects if we are to develop sustainable solutions.

Fortunately, millions of people around the world are taking action to safeguard biodiversity and to preserve and restore Earth's ecological and evolutionary processes. We will explore these efforts more fully in our discussion of biodiversity and conservation biology in Chapter 11. For now, let us see how Hawaiians have been confronting the challenges to their biodiversity.

Introduced species pose challenges for native populations and communities

On top of our direct effects on populations, communities, and ecosystems, human beings exert many indirect effects—for instance, by introducing species into areas where they do not occur naturally. Some such introduced species thrive in their new surroundings, killing or displacing native species (pp. 88–89, 286–289). Island species are particularly vulnerable to introduced species: They have evolved in isolation in small areas with a limited community of other species, and so they lack defenses against mainland species that are well adapted to deal with a broad array of enemies.

The Hawaiian Islands have been utterly transformed by impacts from introduced species. Cattle, goats, sheep, and pigs eat native vegetation, endangering plant populations and altering entire landscapes. Alien grasses, shrubs, and trees spread across the landscapes that livestock have altered. Rat, cats, dogs, and mongooses eat the eggs and young of ground-nesting birds with impunity, and have driven a number of them extinct. Forest birds suffering already from predation and habitat loss now also struggle against diseases like pox and malaria. Pigs have made the malaria problem worse, because they dig holes in the forest floor, where rainwater forms shallow pools in which mosquitoes breed.

As a result, biologists and land managers have found that trying to help a species in trouble often means trying to eradicate or control populations of another that is doing too well. For instance, in many areas pigs are being hunted and pig-free areas are being fenced off. However, pigs are clever animals, and some usually escape. Moreover, native Hawaiian people who hunt pigs have no incentive to get rid of every last pig; otherwise, they could no longer hunt them.

FIGURE 3.20 Hawai'i has protected some of its diverse natural areas, helping to stimulate its economy with ecotourism. Here, a scuba diver observes raccoon butterflyfish at a coral reef along the Kona coast of Hawaii's Big Island.

Innovative solutions are working

Amid all the challenges of Hawaii's extinction crisis, hard work is resulting in some inspirational success stories, and several species have been saved from imminent extinction already. At Hakalau Forest, ranchland is being restored to forest, invasive plants are being removed and native ones are being planted, and nēnē are being protected while new populations of them are being established.

Elsewhere across Hawai'i, tracts of public land are being managed with similar goals and techniques, and some private landholders have joined in conservation efforts. Early work at Hawai'i Volcanoes National Park inspired the work at Hakalau, as well as efforts by managers and volunteers from the Hawai'i Division of Forestry and Wildlife, The Nature Conservancy of Hawai'i, Kamehameha Schools, and local watershed protection groups. People are protecting land, removing alien mammals and weeds, and restoring native habitats. Offshore, conservation efforts are gaining steam as well, as Hawaiians strive to protect their fabulous coral reefs, seagrass beds, and beaches from pollution and overfishing. The northwesternmost Hawaiian Islands are now part of the largest federally declared marine reserve (p. 443) in the world.

Hawai'i and its citizens are reaping benefits from their conservation efforts—economic benefits as well as ecological ones. The islands' wildlife and natural areas draw tourists from around the world, a phenomenon called **ecotourism** (FIGURE 3.20). A large percentage of Hawaii's tourism is ecotourism, and tourism as a whole draws more than 7 million visitors to Hawai'i each year, provides thousands of jobs to Hawaiians, and pumps $12 billion annually into the state's economy.

Climate change now poses an extra challenge

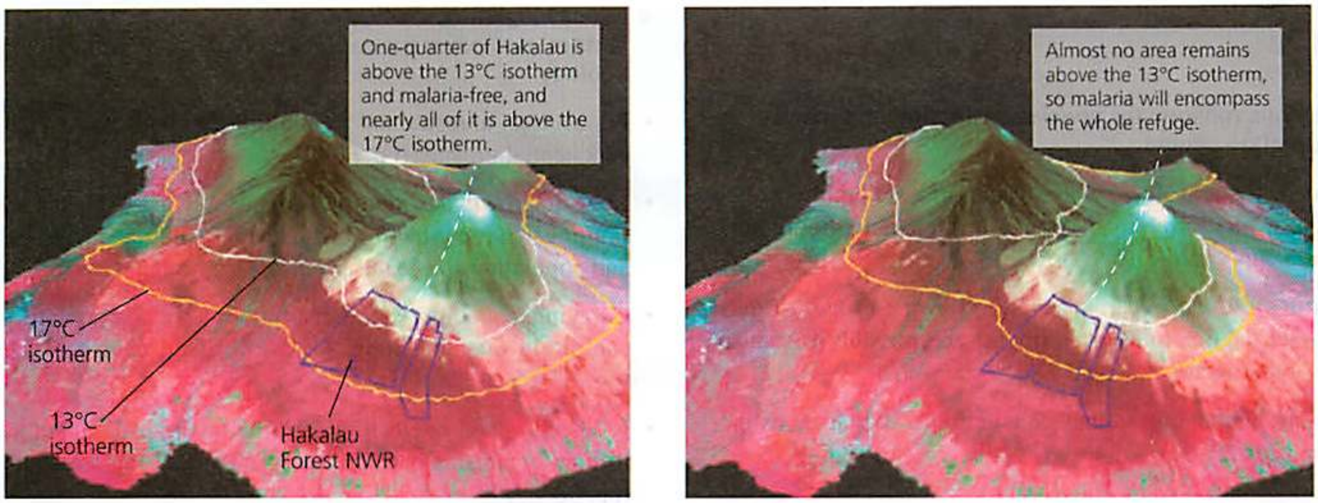
Traditionally, people sought to conserve populations of threatened species by preserving and managing tracts of land (or areas of ocean) designated as protected areas. However, global climate change (Chapter 18) threatens this strategy. As temperatures climb and rainfall patterns shift, conditions within protected areas may turn unsuitable for the species they were meant to protect.

Hawaii's systems are especially vulnerable. At Hakalau Forest on the slopes of Mauna Kea, mosquitoes and malaria are expected to move upslope into the refuge as temperatures rise, exposing more and more birds to disease (FIGURE 3.21). Meanwhile, some researchers maintain that climate change will lower the cloud layer atop Mauna Kea, reducing rainfall at high elevations and pushing the upper limit of the forest downward. If they are correct, Hakalau's honeycreepers may become trapped within a shrinking band of forest by malaria from below and drought from above.

On the Hawaiian island of Kaua'i, the outlook is worse: Forests there are closer to the mountaintops, so climate warming is expected to shift the forests upward until they vanish, leaving their inhabitants nowhere to go. Already mosquitoes have moved upslope and bird populations are diminishing. Two honeycreeper species, the 'akeke'e and the 'akikiki, were recently added to the Endangered Species List (p. 296).

WEIGHING THE ISSUES

HOW BEST TO CONSERVE BIODIVERSITY? Most people view national parks and ecotourism as excellent ways to help keep ecological systems intact. Yet plenty of native Hawaiian creatures face declining populations and the threat of extinction despite living within a reserve, and climate change and disease pay no heed to park boundaries. What lessons can we learn from this about the conservation of biodiversity? Are parks and preserves sufficient? What other approaches might we pursue to save declining species?



(a) Today

(b) With 2°C of climate warming

FIGURE 3.21 **Researchers have modeled how a warming climate will affect the native birds of Hakalau Forest NWR.** Avian malaria cannot survive where temperatures dip below 13°C, and it peaks where summer temperatures average 17°C. Today **(a)**, 24% of Hakalau lies above (cooler than) the 13°C isotherm and is free of malaria. If climate warms by 2°C, however **(b)**, then the isotherms move upslope, and only 1% of Hakalau will remain cooler than 13°C and malaria-free. *Data from: Benning, T.L., et al. 2002. Interactions of climate change with biological invasions and land use in the Hawaiian Islands: Modeling the fate of endemic birds using a geographic information systems.* Proc Natl. Acad. Sci. *99: 14246–14249.*

The challenges of climate change mean that scientists and managers need to come up with new ways to help save declining populations. We will learn about the many efforts being made across the world in our exploration of biodiversity and conservation biology in Chapter 11. In Hawai'i, it remains to be seen how effectively management and ecotourism can stem the tide of challenges and help preserve natural systems in the long term. Resources and efforts to preserve habitat and protect endangered species will likely need to be stepped up. Programs to restore altered communities to their former condition—as is being done at Hakalau Forest—will also be necessary. The restoration of ecological communities is one phenomenon we will examine in our next chapter, as we shift from populations to communities.

Conclusion

The honeycreepers of Hakalau Forest National Wildlife Refuge, along with many other Hawaiian species, have helped to illuminate the fundamentals of evolution and population ecology that are integral to environmental science. The evolutionary processes of natural selection, speciation, and extinction help determine Earth's biodiversity. Understanding how ecological processes function at the population level is crucial to protecting biodiversity threatened by the mass extinction event that many biologists maintain is now underway. Population ecology also informs the study of human populations (Chapter 8), another key endeavor in environmental science.

Reviewing Objectives

You should now be able to:

● Explain natural selection and cite evidence for this process

- Because organisms produce excess young, individuals vary in their traits, and many traits are inherited, some individuals will prove better at surviving and reproducing. Their genes will be passed on and become more prominent in future generations. (p. 50)
- Mutations and recombination provide the genetic variation for natural selection. (p. 50)
- We have produced our pets, farm animals, and crop plants by artificial selection. (p. 52)

● Describe how evolution influences biodiversity

- Natural selection can act as a diversifying force as species adapt to their environments in myriad ways. (pp. 52–53)
- Speciation by geographic isolation (or other means) produces new species. (pp. 53–54)
- The branching patterns of phylogenetic trees reflect the historical pattern in which lineages of organisms have diverged. (p. 54)

- The fossil record informs us about life's history (pp. 55, 58)

Discuss reasons for species extinction and mass extinction events

- Extinction may occur when species that are highly specialized or that have small populations encounter rapid environmental change. (p. 59)
- Earth's life has experienced five known episodes of mass extinction, due to asteroid impact and possibly volcanism and other factors. (p. 59)
- Today, human impact may be initiating a sixth mass extinction. (pp. 59–60)

List the levels of ecological organization

- Ecologists study phenomena on the organismal, population, community, and ecosystem levels—and, increasingly, at the level of the biosphere. (pp. 60–61)
- Habitat, niche, and specialization are important ecological concepts. (p. 61)

Outline the characteristics of populations that help predict population growth

- Populations are characterized by population size, population density, population distribution, sex ratio, and age structure. (pp. 62–63)
- Birth and death rates, as well as immigration and emigration, determine how a population will grow or decline. (p. 66)

Assess logistic growth, carrying capacity, limiting factors, and other fundamental concepts in population ecology

- Populations unrestrained by limiting factors will undergo exponential growth. (pp. 66–67)
- Logistic growth describes the effects of density-dependent limiting factors; growth slows as population size increases, and population size levels off at a carrying capacity. (p. 67)
- Carrying capacity is the maximum size a population can attain over the long term in a given environment. (pp. 67–68)
- K-selection and r-selection describe theoretical endpoints in how organisms can allocate growth and reproduction. (pp. 68–69)

Identify efforts and challenges involved in the conservation of biodiversity

- Social and economic factors influence our impacts on natural systems in complex ways. (p. 69)
- Introduced species are one of many impacts that affect native species and systems, particularly on islands. (pp. 69–70)
- Extensive efforts to protect and restore species and habitats are needed to prevent further erosion of biodiversity. (p. 70)
- Climate change is challenging the effectiveness of protected areas. (pp. 70–71)

Testing Your Comprehension

1. Explain the premises and logic that support the concept of natural selection.
2. Describe two examples of evidence for natural selection.
3. Describe the steps involved in allopatric speciation.
4. Name three organisms that have become extinct or are threatened with extinction. For each, give a probable reason for its decline.
5. What is the difference between a species and a population? Between a population and a community?
6. Define and contrast the concepts of habitat and niche.
7. List and describe each of the five major population characteristics discussed. Briefly explain how each shapes population dynamics.
8. Can a species undergo exponential growth forever? Explain your answer.
9. Describe how limiting factors relate to carrying capacity.
10. Explain the difference between K-selected species and r-selected species. For each, give an example that was not mentioned in the chapter.

Seeking Solutions

1. In what ways has artificial selection changed people's quality of life? Give examples. How might artificial selection be used to improve our quality of life further? Can you envision a way it could be used to reduce our environmental impact?
2. In your region, what species are threatened with extinction? What reasons lie behind their endangerment? Suggest steps that could be taken to bolster their populations.
3. Do you think the human species can continue raising its global carrying capacity? How so, or why not? Do you

think we *should* try to keep raising our carrying capacity? Why or why not?

4. Describe some of the challenges facing native species of plants and animals in Hawai'i. What steps have been taken at Hakalau Forest NWR and elsewhere to address these challenges? What steps do you think biologists and managers will need to take in the future to safeguard native Hawaiian species, populations, and communities?
5. What are some advantages of ecotourism for a state like Hawai'i? Can you think of any potential disadvantages?
6. **THINK IT THROUGH** You are a population ecologist studying animals in a national park, and park managers are asking for advice on how to focus their limited conservation funds. How would you rate the following three species, from most vulnerable (and thus most in need of conservation attention) to least vulnerable? Give reasons for your choices.
   - A bird with an even (1:1) sex ratio that is a habitat generalist
   - A salamander endemic to the park that lives in high-elevation forest
   - A fish that specializes on a few types of invertebrate prey and has a large population size

Calculating Ecological Footprints

Americans love their coffee, whether it comes from Hawaii's Kona region or elsewhere in the world. In 2012, coffee consumption in the United States neared 3.8 billion pounds (out of 19.2 billion pounds produced globally). Next to petroleum, coffee is the most valuable (legal) commodity on the world market, and the United States is its leading importer. Given this data, estimate coffee consumption rates in the table below.

Most coffee in Kona and elsewhere is produced in large plantations, where coffee is the only tree species and is grown in full sun where natural forests have been cut. However, approximately 2% of coffee is produced in smaller groves where coffee trees are intermingled with other species under a partial canopy. These shade-grown coffee plantations maintain greater habitat diversity for birds and other tropical rainforest wildlife.

	Population	Pounds of coffee per day	Pounds of coffee per year
You (or the average American)	1	0.34	12.6
Your class			
Your hometown			
Your state			
United States			

Data from International Coffee Organization.

1. What percentage of global coffee production is consumed in the United States? If U.S. coffee drinkers consumed only shade-grown coffee, how much would shade-grown production need to increase to meet demand?
2. How much extra would you be willing to pay per pound for shade-grown coffee as opposed to standard coffee, if you knew that your money would help to prevent habitat loss for forest-dwelling birds, such as the many songbirds that migrate between Latin America and North America?
3. If everyone in the United States were willing to pay as much extra per pound for shade-grown coffee as you are, how much additional money would that generate for biodiversity conservation in the tropics each year?

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