Module 3.1 Evolution and Extinction: A TROPICAL MURDER MYSTERY

Finding the missing birds of Guam

The brown tree snake (*Boiga irregularis*).

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After reading this module, you should be able to answer these GUIDING QUESTIONS

1. What is biological evolution, and how do populations adapt to changes via natural selection?
2. Why is genetic diversity important to natural selection?
3. What is coevolution, and what problems can emerge when species that did not coevolve

together suddenly share a habitat?
4. How do random events influence the evolution of a population?
5. How do humans, intentionally or accidentally, affect the evolution of a population?
6. What factors affect the pace of evolution and extinction, and why are extinctions that occur quickly more of a concern than those that take a long time to unfold?
7. How do the mass extinction events of the past compare to extinctions during intervening times and today?

On a crisp December morning in 2013, representatives of several federal agencies met on Anderson Air Force Base in Guam — a South Pacific island and U.S. territory — to watch an experiment that sounded more like science fiction than science. As they looked on with binoculars, military personnel in a small fleet of helicopters dropped dead baby mice, one by one, into the surrounding jungle. The mice had been laced with acetaminophen and fitted with lightweight streamers that served as mini parachutes.

WHERE IS GUAM?

The map shows the island Guam in the North Pacific Ocean. China is to the northwest, Philippines to the west, Indonesia to the southwest, New Guinea to the south, and Australia further south of New Guinea. A magnified view of Guam shows the Anderson Air Force Base to the northeast on the island.

The mice could be thought of as paratroopers in a war that the island has been fighting for half a century against a most elusive, yet devastating enemy: brown tree snakes. Introduced accidentally from other Pacific islands to Guam through ships sometime back in the 1940s, they have driven almost all of the island's native bird species to extinction.

The mouse airdrop was part of the effort to decrease the snake population. Acetaminophen is lethal to the snakes. The parachutes would ensure that the mice would catch in the trees, where the snakes live and eat. Operation Mouse Drop is just one of many tools currently employed to address a problem that has plagued wildlife biologists for half a century and that, for years, was shrouded in mystery.

It was the late 1960s when the birds of Guam began dying off with disturbing speed. By the early 1980s, four species had gone extinct, ten others were in danger of joining them, and wildlife experts had no clue why. Biologist Julie Savidge, a PhD student at the University of Illinois, took on the project and headed to Guam. Early hypotheses (diseases or pesticides) didn't pan out, but the locals were certain that brown tree snakes (*Boiga irregularis*), non-native snakes up to 6 feet long, were responsible for the birds' demise. Savidge began to investigate whether these reptiles might be causing the *extinctions*. Surely it was something else; could a few snakes really obliterate a whole island's worth of birds?

extinction

The complete loss of a species from an area; may be local (gone from an area) or global (gone for good).

Dr. Julie Savidge

Dr. Julie Savidge holding a Mariana Fruit-Dove. This species only occurs on certain islands within the Mariana Islands, and the last sighting on Guam was in 1985. This bird was caught as part of an early blood-sampling effort to see if exotic diseases might be causing the bird decline on Guam.

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1 NATURAL SELECTION AS A MECHANISM FOR EVOLUTION

Key Concept 1: Populations can adapt to a changing environment when individuals whose inherited traits make them better suited to survive or reproduce leave more offspring with those traits on average than other less suited individuals — a process known as natural selection.

Before they started disappearing, Guam was home to 18 native species of birds, each specially suited to life on the island.

Populations usually contain individuals that are genetically different from one another. According to the evolutionary theory first put forth by Charles Darwin and Alfred Russel Wallace, a *selective pressure* on a population — a nonrandom influence that affects who survives or reproduces — favors individuals with certain inherited traits over others (such as better camouflage, tolerance for drought, or enhanced sense of smell). These individuals have *differential reproductive success* compared to other individuals: They leave more offspring than those who are less suited for their environment.

selective pressure
: A nonrandom influence that affects who survives or reproduces.

The process by which organisms best adapted to the environment survive to pass on their traits is *natural selection*. Evolutionary biology helps us understand the diversity of life on Earth and how populations change over time. It is one of the pillars of biological sciences and has been elevated to the level of scientific theory (see Module 1.2) by the vast amount of evidence that supports the occurrence of evolution and the mechanisms by which it happens.

natural selection
: The process by which organisms best adapted to the environment survive to reproduce, leaving more offspring than less well-adapted individuals.

For most populations, more offspring are born than can survive, since resources are limited and many species produce large numbers of young. Since only some individuals will survive, over time, the population will contain more and more of these better-adapted individuals and their offspring. Ultimately, this changes how common certain variants of *genes* are in the population (these variants are called *alleles*): The frequency (percentage in the population) of some alleles increases and that of others decreases. When this occurs, the population has experienced *evolution*, or changes in the *gene frequencies* within a population from one generation to the next. Natural selection may be *stabilizing*, *directional*, or *disruptive*, depending on which genetic traits are favored or selected against.

genes
: Stretches of DNA, the hereditary material of cells, that each direct the production of a particular protein and influence an individual's traits.

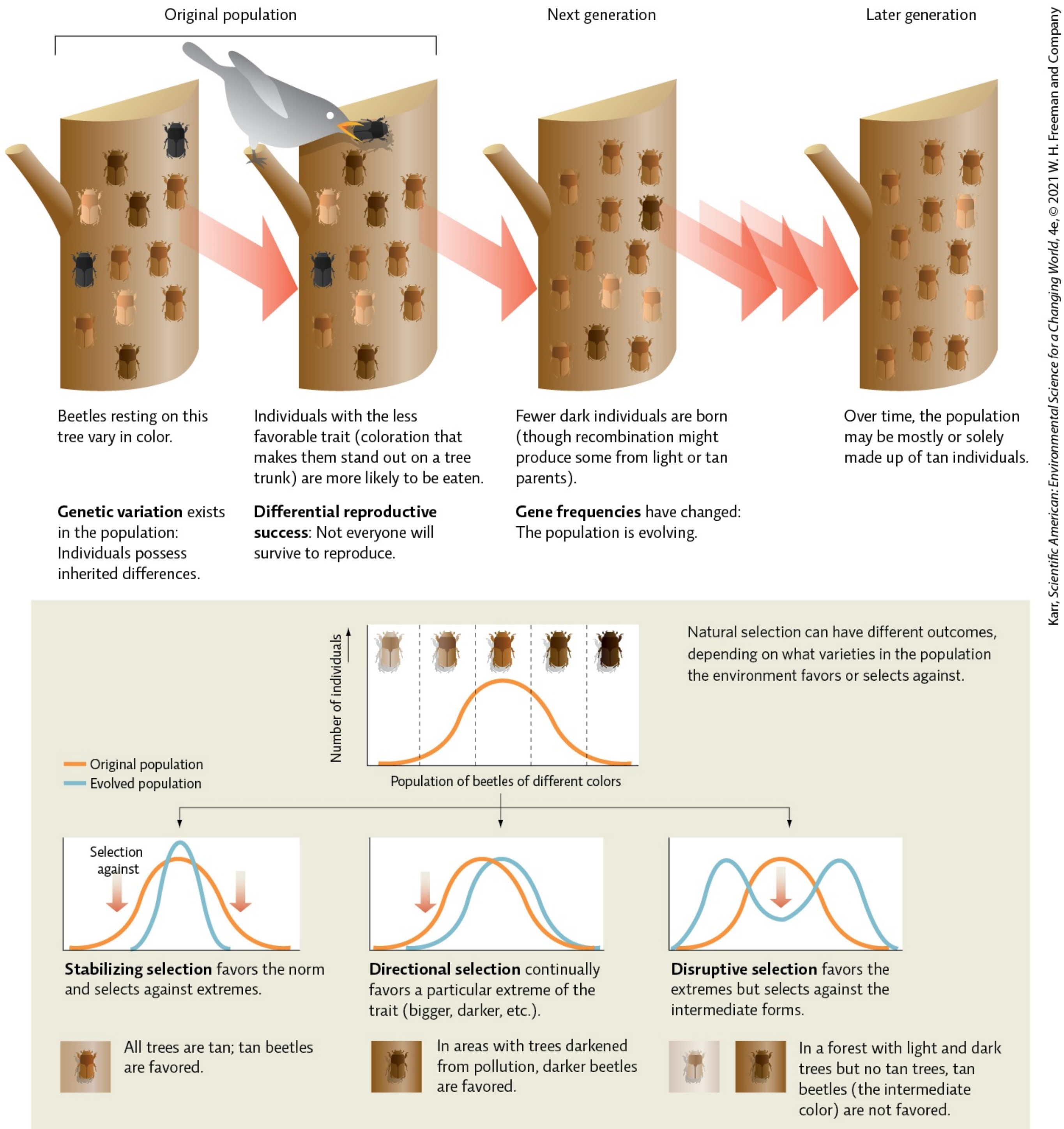
alleles
: Variants of genes that account for the diversity of traits seen in a population.

evolution
: Differences in the gene frequencies within a population from one generation to the next.

gene frequencies
: The assortment and abundance of particular variants of genes relative to each other within a population.

INFOGRAPHIC 1 NATURAL SELECTION AT WORK

When the environment presents a selective force (e.g., a new predator, changing temperatures, change in food supply), natural selection is the primary force by which populations adapt. The survivors are those who were lucky enough to have genetic traits that allowed them to survive in their changing environment. (Others who did not possess the trait were not as likely to survive to reproduce.) Because survivors pass on those adaptations to their offspring, the gene frequencies of the population change in the next generation, which means some traits are more common and others are less common than they used to be. When this happens, the population is said to have evolved.



The series of four illustrations show tree trunks with different colored beetles. The first two tree trunks are labeled, original population. The first tree trunk shows black, light, tan, and dark colored beetles. A text below reads, “Beetles resting on this tree vary in color. Genetic variation exists in the population: Individuals possess inherited differences.” The second tree trunk shows same colored beetles with a bird trying to eat a black beetle. A text below reads, “Individuals with the less favorable trait (coloration that makes them stand out on a tree trunk) are more likely to be eaten. Differential reproductive success: Not everyone will survive to reproduce.” The third tree trunk is labeled, next generation, and shows the tree trunk with light, tan, and dark colored beetles. A text below reads, “Fewer dark individuals are born (though recombination might produce some from light or tan parents). Gene frequencies have changed: The population is evolving.” The fourth tree trunk is labeled, later generation, and shows the tree trunk with light and tan colored beetles. A text below reads, “Over time, the population may be mostly or solely made up of tan individuals.” A text beside the first graph at the top reads, “Natural selection can have different outcomes, depending on what varieties in the population the environment favors or selects against.” The horizontal axis represents population of beetles of different colors and is divided into five equal segments with lighter to darker shade beetles from left to right. The vertical axis represents number of individuals and increases from bottom to top. The bell-shaped curve representing original population starts from first segment, peaks at third segment, and ends at the fifth segment. This graph leads to three graphs at the bottom comparing original population with the evolved population. In the first graph: the bell-shaped curve for evolved population is narrower than original with a nonexistent dark and light beetle population. Two downward arrows pointing to the slopes of original population curve read, “Selection against.” A text below reads, “Stabilizing selection favors the norm and selects against extremes.” A corresponding illustration shows a tan colored beetle with a text that reads, "All trees are tan; tan beetles are favored." In the second graph: the bell-shaped curve for evolved population is similar to the original but slightly shifted to the right, showing a further minimized light beetle population. A downward arrow points to the left slope of original population. A text below reads, “Directional selection continually favors a particular extreme of the trait (bigger, darker, etc.).” A corresponding illustration shows a dark colored beetle with a text that reads, " In areas with trees darkened from pollution, darker beetles are favored." In the third graph: the curve for evolved population shows two peaks instead of one, with a low trough in the middle for the population of tan beetles and peaks for the population of light tan and dark beetles. A downward arrow points to the trough. A text below reads, “Disruptive selection favors the extremes but selects against the intermediate forms.” A corresponding illustration shows a light and a tan colored beetle with a text that reads, "In a forest with light and dark trees but no tan trees, tan beetles (the intermediate color) are not favored.”

Identify the gene frequencies of the “original population” for each color morph (dark gray, dark brown, light brown, dark tan, and light tan) by counting the number of each and expressing it as a percentage of the whole. Now do the same for the “later generation.” Has evolution occurred? Explain.

It is important to note that *individuals* are selected but *populations* evolve; individuals do not change their own genetic makeup to produce new necessary adaptations, such as bigger size or pesticide resistance. If they get the opportunity to reproduce, they pass on their traits to the next generation. If they cannot tolerate environmental changes, as was the case with the first bird species to disappear from Guam (the bridled white-eye), they die or fail to reproduce and do not pass on their genes. Individuals may be able to adjust their behavior to accommodate environmental changes, but if a trait is not genetically controlled, and therefore is not heritable, it cannot be passed on to the next generation.

Bill Gozansky/Alamy

Green anoles in Florida are evolving in response to the presence of the non-native brown anole from Cuba. These two lizard species compete for the same food in the same area of the trees in which they hunt. The larger brown anole is winning out, pushing the green anole higher up in the tree—a more difficult hunting ground. Directional selection is favoring green anoles with larger toepads, a trait that allows them to better grip the thinner branches higher up in the trees.

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2 GENETIC DIVERSITY AND NATURAL SELECTION

Key Concept 2: Genetic diversity in a population is the raw material on which natural selection operates. The more diverse a population, the more likely there will be individuals present who can withstand or even thrive if environmental conditions change.

The ability of a population to adapt is a reflection of its tolerance limits to environmental factors, which largely depend on *genetic diversity* — different individuals having different alleles. A population that is highly diverse (has individuals with many inherited differences) is likely to have wider tolerance limits (see Infographic 4 in Module 2.1), which increases the population's potential to adapt to changes. This means it is more likely that some individuals will exist that can withstand (or even thrive in) the changes and that the population as a whole will survive. If a change occurs that produces a condition outside the range where individuals can survive and reproduce (for instance, the climate becomes warmer than anyone can tolerate), the population will die out. Similarly, if a new challenge is presented, such as the introduction of a new predator or competitor, the survival of the population will depend on whether there are any individuals in the population who can effectively deal with the new species. If the snakes on Guam were indeed responsible for killing the birds, any birds that happened to have effective snake-avoidance behaviors would have had a greater chance of survival.

genetic diversity
: The heritable variation among individuals of a single population or within a species as a whole.

Robert Hamilton/Alamy/Diomedia

These Asian lady beetles show genetic diversity—the raw material on which natural selection works.

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Two main sources of variation can increase genetic diversity in a population. The ultimate source of new variability is genetic *mutation*, a change in the DNA sequence in the sex cells that alters a gene, sometimes to the extent that it produces a new trait. Mutations are rare, but because DNA replication and repair occur all the time, these rare events add up. When a mutation produces traits that are beneficial, they can quickly be passed on to the next generation, allowing the population to evolve to be better adapted to its environment. A second source of genetic variety occurs as eggs and sperm are made: *Genetic recombination* shuffles alleles around and sometimes produces individuals with new traits when a sperm fertilizes an egg.

The value of this genetic diversity is illustrated today in the example of the rock pocket mouse of the American Southwest desert. Animals of this species have coats that are either light tan or a darker color. It turns out that coat color corresponds to a population's environment: Areas of light-colored rock contain populations with mostly tan mice, whereas darker mice inhabit black lava rock regions. Research by evolutionary biologists Hopi Hoekstra and Michael Nachman has shown that coat color is determined by a single gene that comes in two different alleles. The dominant allele is designated by the uppercase letter D; the recessive allele is designated by the lowercase letter d. All individuals have two copies of the gene, and the color of their coat is determined by which two alleles they possess. Darker mice have at least one dominant allele (DD or Dd). Tan mice possess two recessive alleles (dd).

It is likely that coat color provides camouflage and protection from visual hunters, but only if the mouse is on a background of the same color. A study on deer mice (a similar species) showed that predatory owls are more successful at capturing mice on a contrasting background. This gives support to the conclusion that coat color is adaptive as camouflage and therefore is responsive to natural selection. (See Section 3 of Module 3.2 for another example of the importance of genetic diversity — the potato famine in 19th-century Ireland.)

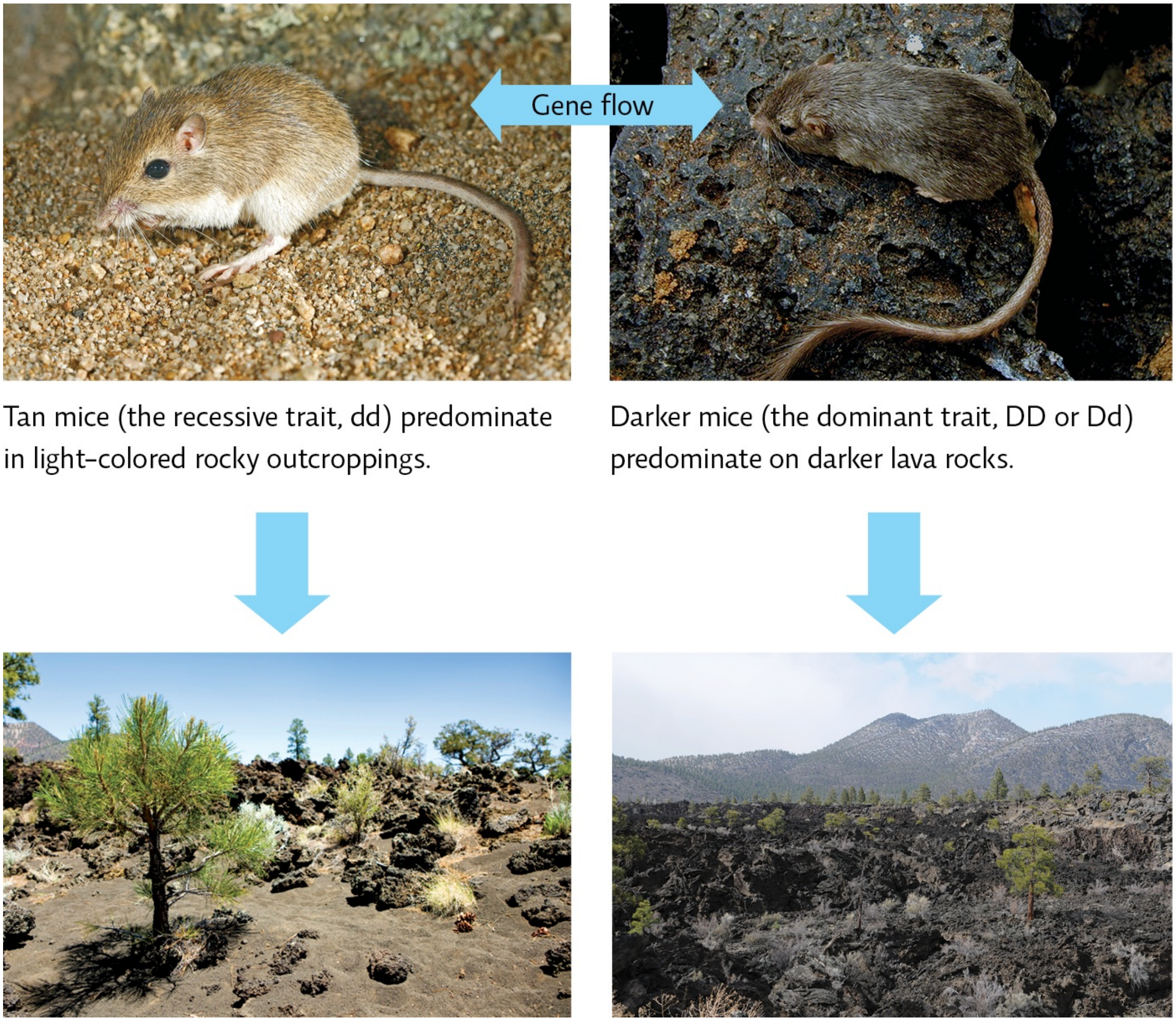
INFOGRAPHIC 2 EVOLUTION IN ACTION

Natural selection produces populations with different gene frequencies (more or less of a particular gene variant or allele). For this to occur, there must be genetic variation (more than one allele for a given trait) and a selective pressure (a reason one variant is better than another in a given situation).

Different color morphs of the rock pocket mouse (*Chaetodipus intermedius*) are found on different-colored rocky outcroppings in the desert Southwest. An evaluation of the mice living on or near the Pinacate lava flow in southern Arizona represents the first documentation of the genetic basis (in this case, a single gene) for a naturally favored trait. The well-known peppered moth is another example in which different color variants are favored in different habitats, but the genes responsible for that trait have not yet been identified.

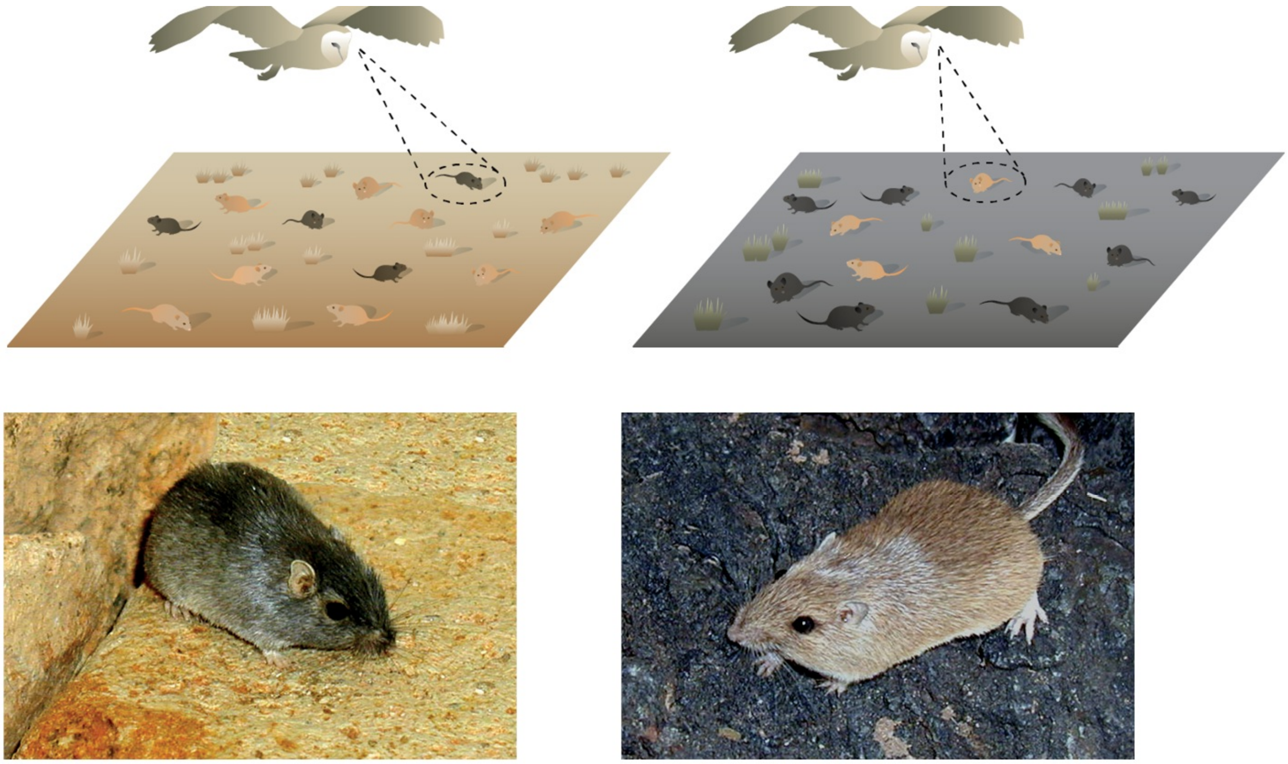
Even though there is gene flow between dark and light populations that are close to each other, populations on tan rock have mostly tan individuals, and populations on dark rock have mostly dark individuals, suggesting a strong selective pressure that favors one color over the other.

Predatory owls are likely the selective pressure that favors different coat colors in different habitats.



A study done with dark and light varieties of deer mice revealed that owls caught twice as many opposite-colored mice (dark mice on a light background or tan mice on a dark background) as mice whose coloration matched their background, even in almost total darkness. Owl predation is therefore likely to be a strong selective pressure on coat color, driving directional selection that produces either light or dark populations of mice, depending on the background.

The first photo shows a tan mouse and accompanying text reads, “Tan mice (the recessive trait, small D small D) predominate in light-colored rocky outcroppings.” A double-headed arrow labeled, gene flow, points to the second photo that shows a dark brown mouse and accompanying text reads, “Darker mice (the dominant trait, big D big D or big D small D) predominate on darker lava rocks.” A downward arrow from the first photo leads to the third photo that shows a light brown desert environment. A downward arrow from the second photo leads to the fourth photo that shows a dark brown rocky environment.



The first illustration shows several light and dark colored mice in a light environment. A hawk flying above locates a dark colored mouse. The second illustration shows several light and dark colored mice in a dark environment. A hawk flying above locates a light colored mouse. The first photo shows a dark colored mouse on a light surface and the second photo shows a light colored mouse on a dark surface.

If this mouse population migrated to an area with a red rock habitat with visual predators like hawks or owls, what could prevent the population from evolving into one with red coats?

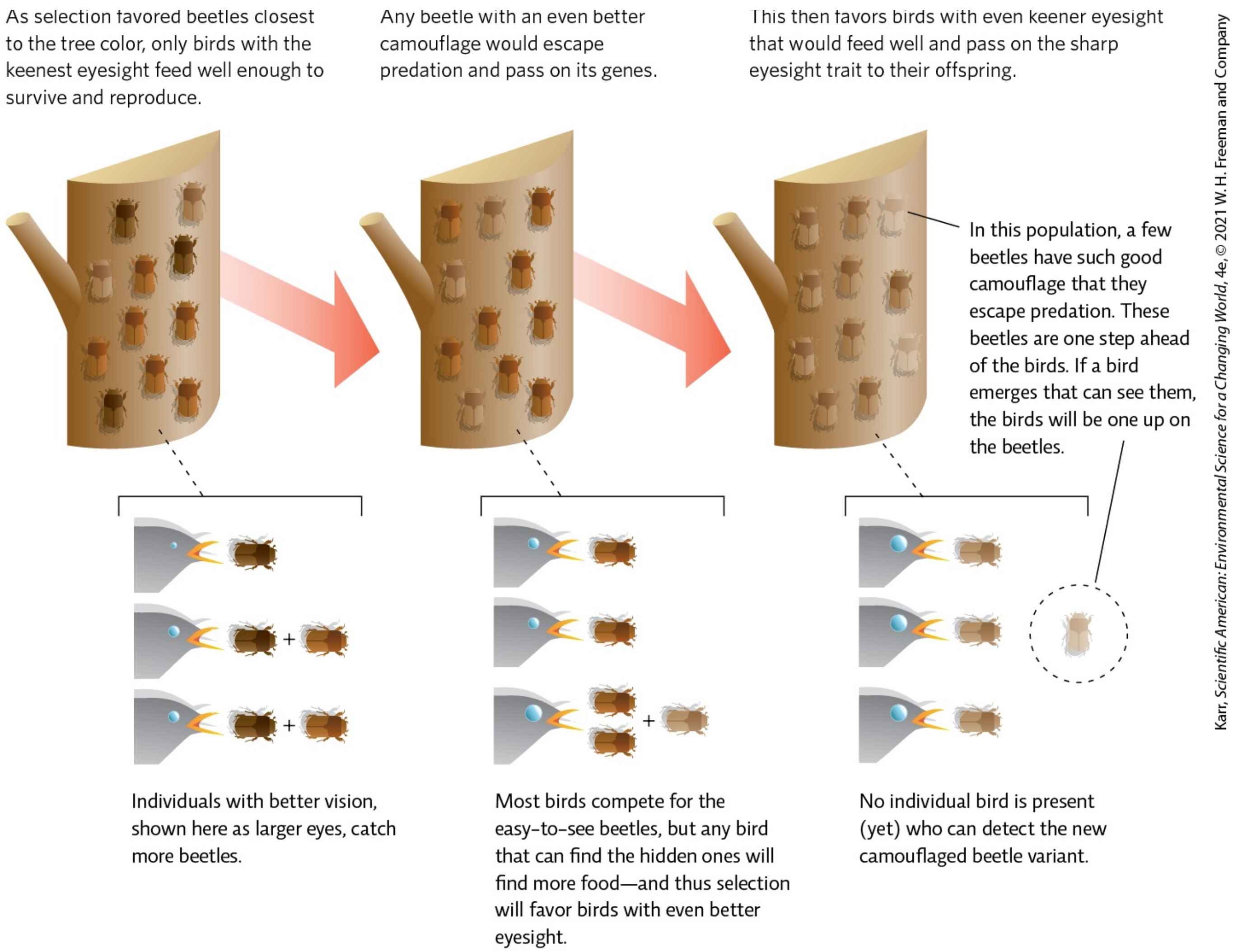
3 COEVOLUTION

Key Concept 3: Two species can become highly adapted to each other when each becomes the selective pressure that favors certain traits in the other, a process known as coevolution. Species that never coevolved with a particular predator or competitor may not have the traits needed to survive if that species invades their habitat.

A special type of natural selection, known as *coevolution*, occurs when two species each provide the selective pressure that determines which of the other's traits are favored by natural selection. Predator and prey species usually evolve together, each exerting selective pressures that shape the other. As predators get better at catching prey, the only prey to survive are those a little better at escaping, and it is those individuals that reproduce and populate the next generation. This game of one-upmanship continues generation after generation, with each species affecting the differential survival and reproductive success of the other. The result can be a predator extremely well equipped to capture prey and prey extremely well equipped to escape.

coevolution
: A special type of natural selection in which two species each provide the selective pressure that determines which traits are favored by natural selection in the other.

INFOGRAPHIC 3 COEVOLUTION ALLOWS POPULATIONS TO ADAPT TO EACH OTHER



What do you predict would happen to the original beetle population if a species of bird with extremely keen eyesight (like those shown on the right side of the diagram) were accidentally introduced into the beetle's habitat?

A text above the first infographic reads, “As selection favored beetles closest to the tree color, only birds with the keenest eyesight feed well enough to survive and reproduce.” An illustration shows a tree trunk with one light, seven tan, and three dark colored beetles. An illustration below shows three birds eating beetles. The first bird with small eyes eats a dark colored beetle; the second and the third birds with larger eyes eat a dark and a tan colored beetles. A text below reads, "Individuals with better vision catch more beetles." A text above the second infographic reads, “Any beetle with an even better camouflage would escape predation and pass on its genes.” An illustration shows a tree trunk with few light and more dark colored beetles. An illustration below shows three birds eating beetles. The first bird with small eyes eats a dark colored beetle; the second bird with big eyes eats a dark colored beetle; and the third birds with larger eyes eat two dark and a light colored beetles. A text below reads, "Most birds compete for the easy-to-see beetles, but any bird that can find the hidden ones will find more food—and thus selection will favor birds with even better eyesight." A text above the third infographic reads, “This then favors birds with even keener eyesight that would feed well and pass on the sharp eyesight trait to their offspring.” An illustration shows a tree trunk with medium, light, and lighter colored beetles. An illustration below shows three birds with large eyes eating a medium colored beetle, each. A lighter beetle is present beside them and is labeled along with the lighter beetles on the tree trunk as, “In this population, a few beetles have such good camouflage that they escape predation. These beetles are one step ahead of the birds. If a bird emerges that can see them, the birds will be one up on the beetles.” A text below reads, " No individual bird is present (yet) who can detect the new, camouflaged beetle variant."

Non-native species that cause ecological, economic, or human health problems and are hard to eradicate are considered *invasive species*, and they can cause significant damage in areas they invade. In fact, invasive species are one of the leading causes of species endangerment worldwide (see Module 3.2).

invasive species
: A non-native species (a species outside its range) whose introduction causes or is likely to cause economic or environmental harm or harm to human health.

Malcolm Schuyl/Alamy

Many ground-nesting birds and turtles in Hawaii have no defenses against this invasive mongoose, a skilled predator that eats their eggs and hatchlings.

If the birds on Guam were indeed eradicated by the invasive snake species, it was because the speed at which the eradication happened prevented the bird populations from potentially coevolving survival strategies to deal with the new snake population. The brown tree snake was already well adapted to preying on birds. But Guam's bird populations had never faced such a predator and had no natural defenses. It was an unfair fight. And like populations worldwide that are isolated on islands or mountaintops or by fragmented habitats, Guam's populations were further handicapped by their isolation; they rarely, if ever, received new individuals from populations elsewhere. Indeed, some of Guam's species were *endemic* — found nowhere else — so no other populations even existed to contribute new members that might be better adapted to the snake.

endemic
: Describes a species that is native to a particular area and is not naturally found elsewhere.

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Some of Guam's bird species went extinct sooner than others. For instance, the endemic bridled white-eye, the gregarious bird species that was extinguished first, was very small, raising the possibility that the small size of these birds might have put them at a disadvantage. Larger species like flycatchers survived longer, though most of them, too, eventually disappeared. Other bird species experienced *extirpation*; the Guam rail, for instance, is gone from Guam, but other populations still live on the nearby island of Rota. If some individuals of the bridled white-eye or other extinct species had been able to avoid the snake (perhaps due to a heritable trait that made them more wary of the predator), their descendants might have produced new populations that could cohabitate with the snake.

extirpation
: Locally extinct in one geographic area but still found elsewhere.

When populations diverge because of isolation, food availability, new predators, or habitat fragmentation that prevents the ability of population members to freely interbreed, new species may arise (*speciation*). This increases the number of species in a community and sometimes produces specialists that can exploit open niches. This separation may be physical (e.g., geographic boundaries the individuals won't cross) or may arise when something prevents some individuals from choosing others as mates, as may happen when individuals spend their time in different parts of their habitat. However, not all evolution is driven in this manner. Random events play a role, too, typically by decreasing genetic diversity rather than increasing it.

4 RANDOM EVENTS AND EVOLUTION

Key Concept 4: Along with natural selection, random events such as genetic drift, the bottleneck effect, and the founder effect also influence the evolution of a population.

In *genetic drift*, some traits (alleles) are passed on or lost by random chance, not because they were selected for (or against), as with natural selection. How could this happen? Even with natural selection at work, in each generation, some individuals may leave more offspring than others, not because they were better adapted to their environment but because they "got lucky" — perhaps due to favorable external factors they mated more, had more offspring, or had more offspring survive. Others might be "unlucky" — they might be in the wrong place at the wrong time (e.g., killed by a mudslide) before having a chance to mate. Just because natural selection would favor certain traits over others, doesn't mean every "better" individual will leave more progeny than all the less well-adapted individuals; the best traits might increase one's chances of survival or reproduction, but no trait guarantees it.

genetic drift

The change in gene frequencies of a population over time due to random mating that results in the loss of some gene variants.

Small populations are much more likely to experience genetic drift than large ones because the offspring of a few "lucky" individuals will have a greater impact on the gene frequencies of the next generation in a small population than a few "lucky" individuals in a large population. In large populations, the effect of genetic drift is more likely to be masked by all the better-adapted individuals who are favored by natural selection and successfully reproduce. In small populations, genetic drift can quickly lead to losses in genetic variability that produce major evolutionary changes in a population.

Genetic drift is more likely to happen if a population has experienced a reduction in size as occurs with the *bottleneck effect*. When only a subset of the original variants reproduces, they can give rise to a new population that is different from the original population. The bottleneck effect can occur when a portion of the population dies, perhaps because of a natural disaster like a flood or because of a strong new selective pressure, such as the introduction of a new predator. The survivors then produce a new generation, and any alleles that were found only in the deceased individuals are lost from the population forever.

bottleneck effect

The situation that occurs when population size is drastically reduced, leading to the loss of some genetic variants and resulting in a less diverse population.

The *founder effect* also reduces population size and therefore available alleles. Consider the situation in which a small subset of a population colonizes a new area. If this subset (the founding population) happens to be less genetically diverse than the original and if the subset becomes completely isolated from the original group such that there is no mixing of the two populations (and no chance to reintroduce those missing alleles), the founding population will produce a population that has different gene frequencies than the original population. (See Module 3.2 for more on the effect of isolation.)

founder effect
: The situation that occurs when a small group with only a subset of the larger population's genetic diversity becomes isolated and evolves into a different population, missing some of the traits of the original group.


Susan Karr

The descendants of the giant tortoises of the Galápagos Islands, which might have arrived at these isolated islands on floating vegetation, have evolved into distinct populations. The larger domed-shelled tortoises, like this one living on Santa Cruz, are found in areas with abundant plant life. The saddle-backed tortoises are adapted to arid regions with less food; their shell is angled upward in the front, allowing the animal to stretch its neck higher in search of food.

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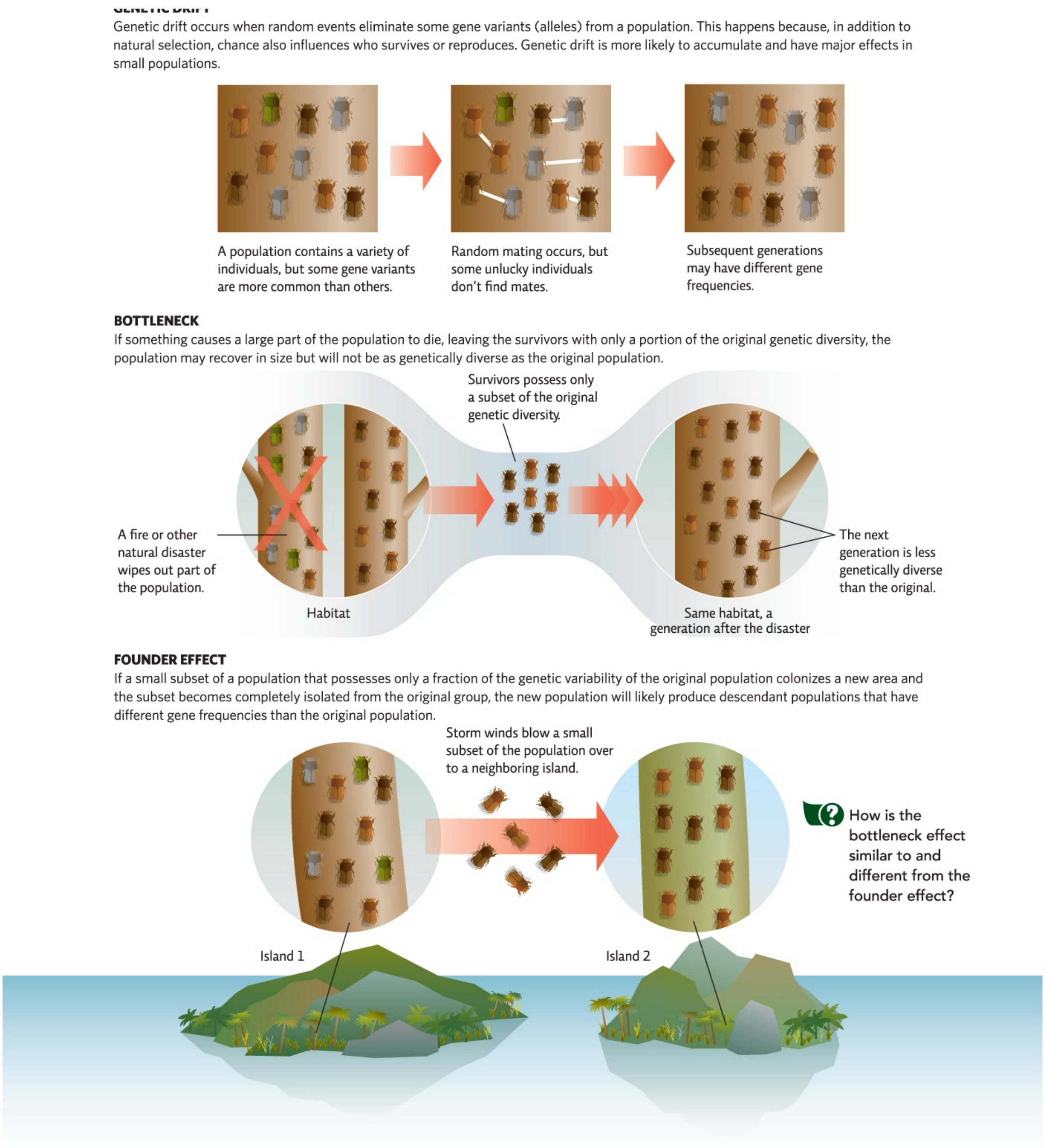
Today human impact increases instances of both the founder effect and the bottleneck effect. Much of what we do isolates populations into smaller groups, forcing them into these situations.

INFOGRAPHIC 4 RANDOM EVENTS CAN ALTER POPULATIONS THROUGH GENETIC DRIFT



First infographic: Three illustrations show differently colored beetles on tree trunks. An arrow points from the first trunk to the second and from the second trunk to the third. The first tree trunk shows one green, three gray, four tan, and three dark colored beetles. A text below reads, “A population contains a variety of individuals, but some gene variants are more common than others.” The second tree trunk shows all the beetles paired with each other except for the green colored beetle. A text below reads, “Random mating occurs, but some unlucky individuals don’t find mates.” The third tree trunk shows only gray, tan, and dark colored beetles. A text below reads, “Subsequent generations may have different gene frequencies.” Second infographic: An illustration shows two tree branches labeled, Habitat, with the first branch showing green, gray, tan, and dark colored beetles. This tree trunk is crossed out and a text reads, “A fire or other natural disaster wipes out part of the population.” The second tree trunk shows tan and dark colored beetles. A rightward arrow points to a group of tan and dark colored beetles and a text reads, “Survivors possess only a subset of the original genetic diversity.” Another rightward arrow points to a tree trunk labeled, Same habitat, a generation after the disaster, and shows several tan and dark colored beetles. A text pointing to the beetles reads, “The next generation is less genetically diverse than the original.” Third infographic: Two illustrations show an island with an enlarged view of a tree trunk. Island 1 shows a tree trunk with green, gray, tan, and dark colored beetles. A rightward arrow overlaid with tan and dark colored beetles point to Island 2. A text reads “Storm winds blow a small subset of the population over to a neighboring island.” Island 2 shows a tree trunk with tan and dark colored beetles.

How is the bottleneck effect similar to and different from the founder effect?

5 ARTIFICIAL SELECTION

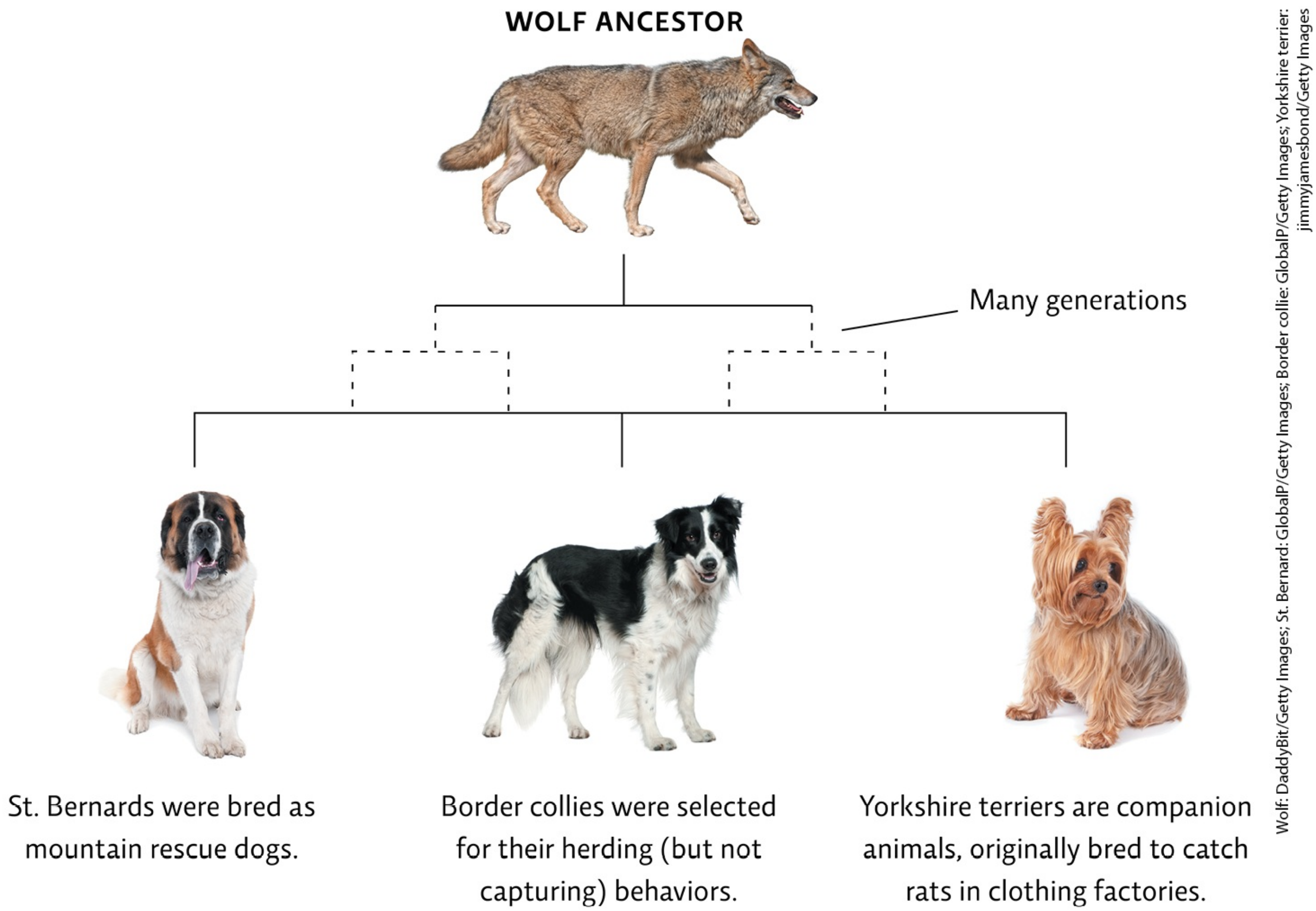
Key Concept 5: In artificial selection, humans choose which traits to keep and which to eliminate from a population through selective breeding. Our actions have also inadvertently led to the evolution of antibiotic- or pesticide-resistant populations.

The introduction of the brown tree snake to Guam was an accident: A snake hitchhiker crossed the ocean on a ship and landed in a veritable bird buffet. But humans also directly affect the evolution of a population through *artificial selection*. Artificial selection works the same way as natural selection, but the difference is that the selective pressure is us (humans). For many animal and plant species, humans choose who breeds with whom in an attempt to produce new individuals with desired traits. By doing this over many generations, people have accentuated certain plant and animal traits, sometimes to extremes. For instance, artificial selection created domestic dogs from their wolf ancestors.

artificial selection
: A process in which humans decide which individuals breed and which do not in an attempt to produce a population of plants or animals with desired traits.

INFOGRAPHIC 5 HUMANS USE ARTIFICIAL SELECTION TO PRODUCE PLANTS OR ANIMALS WITH DESIRED TRAITS

All dogs *(Canis lupus familiaris)* are descendants of the wolf *(Canis lupus)*. By only breeding those males and females with the traits desired (size, herding ability, protective instinct, etc.), humans have created more than 170 dog breeds.



The flowchart starts with a wolf ancestor and branches out downward. The branches are labeled, many generations. The flowchart ends with three descendants: St. Bernards were bred as mountain rescue dogs; Border collies were selected for their herding (but not capturing) behaviors; and Yorkshire terriers are companion animals, originally bred to catch rats in clothing factories.

Why can we say that artificial selection is goal-directed but natural selection is not?

But evolution is ever at work. Pesticide- and antibiotic-resistant populations can emerge as an inadvertent human-influenced selection. When we apply a chemical that kills a pest or pathogen, some individuals survive because of their natural genetic resistance; that is, the individuals were already resistant even though they had never encountered the chemical. These survivors are then the only individuals who reproduce, producing the next generation that is also pesticide-resistant, ultimately changing the frequency of resistant genes in the population (see Infographic 5 in Module 8.1).

6 THE PACE OF EVOLUTION AND EXTINCTION

Key Concept 6: The pace of evolution and extinction is generally slow and is affected by population size and genetic diversity, reproductive rate, generation time, and the strength of the selective pressures at play. When extinctions unfold over long periods of time, better-adapted species tend to replace their predecessors and the niche remains filled; rapid extinction events may eliminate well-adapted species and break important community connections.

The pace of evolution by natural selection is not constant or the same for all species, but in general, it is slow — changes accumulate over generations, and speciation events can take thousands or millions of years. Evolution's pace is affected by a variety of factors, including population characteristics such as the genetic diversity and size of the population, aspects of the species' biology such as its biotic potential (maximum reproductive rate) and generation time, and the strength of the selective pressure a population is facing.

As mentioned earlier, genetic diversity is important because it provides options for natural selection to favor or select against. If a new selective pressure favors a less common trait in the population or if a new favorable trait arises, it can quickly displace other variants in subsequent generations, resulting in evolution of the population. If this results in a speciation event, it can eliminate an ancestral species. When this happens — when a new species replaces an ancestral one — the outcome is unlikely to negatively impact the ecosystem because the niche is still filled.

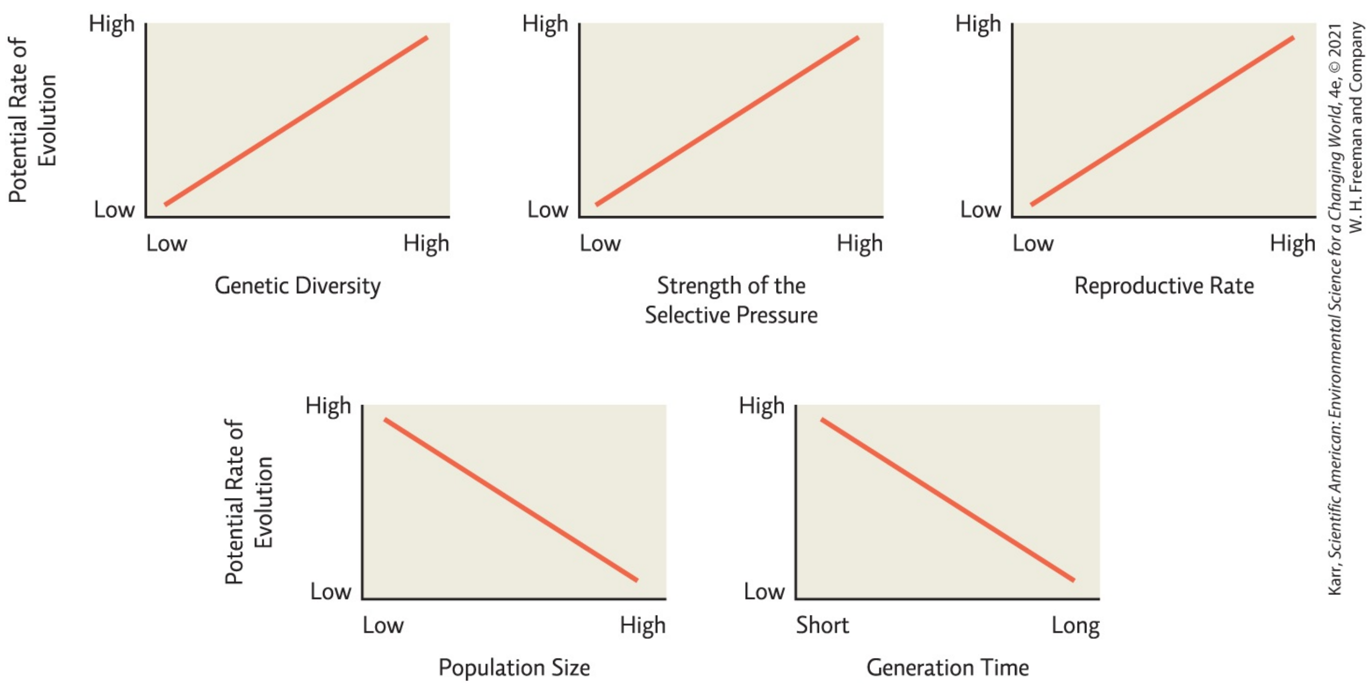
In addition to genetic diversity, the size of the population also makes a difference in how quickly natural selection can produce a change in a population: Beneficial traits can spread more quickly in smaller populations simply because it is more likely that the individuals with the trait will find each other and mate (as long as it is not a population that is widely dispersed). Of course, as mentioned earlier, smaller populations can also be at a higher risk of extinction because they likely contain less genetic diversity.

Reproductive rate and generation time also influence how quickly a population can adapt to changes. Populations of *r*-selected species (those with high reproductive rates and fast generation times) decimated by a disturbance or a depleted resource can quickly bounce back and repopulate the area because the remaining individuals can produce so many offspring in a single breeding cycle. Many *endangered species* (species in high danger of becoming extinct; see Module 3.2), on the other hand, are *K*-selected species, with slower reproductive rates and longer generation times; therefore, they take longer to recover if population numbers fall. Selective pressures that change over the course of just a few years can eliminate a species with a generation time of many years — there is simply not enough time for those able to withstand the stressor to grow up and produce progeny who can also withstand the stressor. (For more on *r*- and *K*-selected species, see Module 2.2.)

The strength of the selective pressure also affects how quickly natural selection might produce a change in a population. One of the reasons the demise of birds in Guam was so stupefying was that it happened so quickly — particularly for the small birds, which were easiest for the snakes to eat. Larger birds disappeared later, when the snakes started eating their nestlings and eggs.

INFOGRAPHIC 6 THE PACE OF EVOLUTION

The speed at which evolution can occur is influenced by a variety of factors. While the relationships below are not guaranteed to affect the rate of evolution as shown (e.g., even a population with high genetic diversity would not be able to evolve [or survive] if no one in the population could withstand the environmental disturbance experienced), in general, the following correlations are seen.



The vertical axis of all graphs represents potential rate of evolution and is labeled low at the bottom and high at the top. The horizontal axis of the first graph represents genetic diversity and is labeled low at the left and high at the right. A positive slope starts from (low, low) and ends at (high, high). The horizontal axis of the second graph represents strength of the selective pressure and is labeled low at the left and high at the right. A positive slope starts from (low, low) and ends at (high, high). The horizontal axis of the third graph represents reproductive rate and is labeled low at the left and high at the right. A positive slope starts from (low, low) and ends at (high, high). The horizontal axis of the fourth graph represents population size and is labeled low at the left and high at the right. A negative slope starts from (low, high) and ends at (high, low). The horizontal axis of the fifth graph represents generation time and is labeled low at the short and long at the right. A negative slope starts from (short, high) and ends at (long, low).

Which of the factors shown are positively correlated with the potential rate of evolution, and which are negatively correlated?

To determine whether the snakes were a strong selective pressure on the birds of Guam, Savidge first had to be sure the snakes actually ate birds. To test this, she set out bird-baited traps around Guam and on nearby Cocos Island (which has no brown tree snakes). What she found shocked her: “In one area [on Guam] where the birds were extinct, 75% of my traps got hit within 4 nights,” she recalls. On Cocos, all the birds used as bait survived. Surveys of Guam’s abundance of small mammals also revealed heavy predation pressure by the snakes — mice and shrews had declined by 94%.

All in all, Savidge amassed three lines of evidence that convinced her that she had finally solved the mystery of Guam’s disappearing birds: The geographic location of the snakes correlated strongly with the birds’ disappearance, brown tree snakes were willing to eat birds, and other small mammals also went missing after the snakes’ arrival. Brown tree snakes, she concluded, were the culprit.

The hunting skill of the snake and the lack of antipredator behaviors in the birds made this new predator a strong selective pressure; a less proficient predator or one whose hunting style was familiar to the birds would have been a weaker selective pressure. Indeed, one lesson of the brown tree snake invasion is that while speciation typically occurs at a slow pace, extinction can occur much more quickly if the rate of change exceeds the ability of the population to adapt. These rapid extinction events are a concern because they can break community connections and leave unfilled niches, negatively impacting other species. This is, in fact, already occurring.

Twelve native bird species are now extinct or extirpated on Guam, including all fruit-eating birds. This is having dire consequences for the island’s trees, according to a 2017 study by Iowa State University researcher Haldre Rogers. Around 70% of Guam’s trees are fruit producers and depend on mutualistic partners for seed dispersal; unfortunately, in Guam, no other species have stepped in to fill this role. Rogers and her team estimate the growth of new trees could be down by as much as 90% due to failed germination of seeds. On the other hand, Rogers’s research has also revealed that spiders are flourishing without enough birds around to keep their numbers in check. Guam’s forests are changing drastically, all because a few snakes found their way to this island.

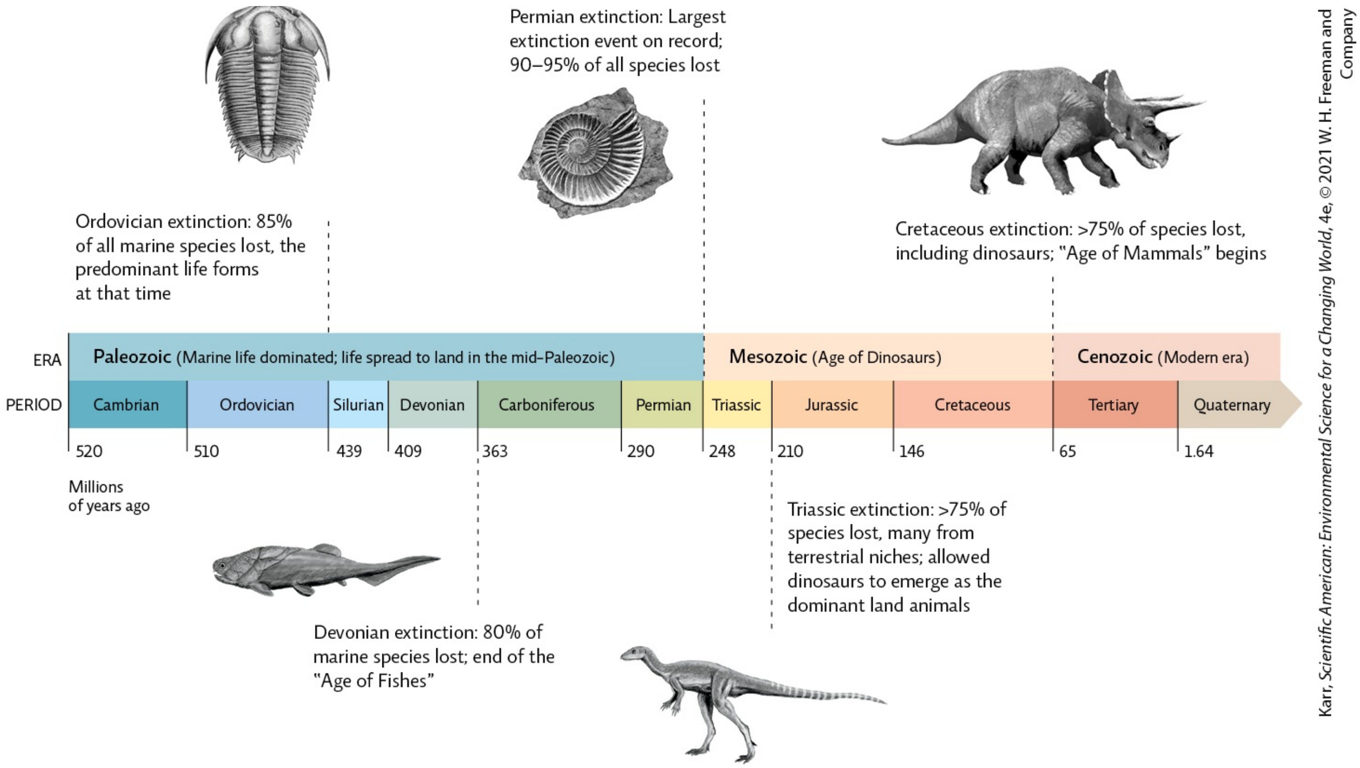
7 MASS EXTINCTIONS: PAST AND PRESENT

Key Concept 7: Extinction rates were much higher in mass extinction events than at other times. Past mass extinctions are linked to natural causes; today human impact appears to be causing another mass extinction.

Extinction is nothing new on Earth. By most estimates, more than 99% of all species that ever lived on the planet have gone extinct. Based on a critical analysis of the fossil record, scientists agree that there have been five *mass extinction events* — when species have gone extinct at much greater rates than during intervening times, each event leading to the loss of 75% or more of the species present on Earth. The most infamous of these was the extinction event that occurred at the transition from the Cretaceous to the Tertiary period, 65 million years ago. Most scientists agree this event was set off by an asteroid impact in the Gulf of Mexico; more than 75% of all species, including the dinosaurs, were wiped out.

INFOGRAPHIC 7A EARTH'S MASS EXTINCTIONS

There have been five mass extinctions in Earth's history, defined as extinction events that eliminated a large number of species in a short period of time (geologically speaking). Each is believed to have been caused by major environmental changes such as the meteor that struck Earth at the end of the Cretaceous period.



A horizontal timescale representing geological periods from left to right reads: Cambian from 520 to 510 millions of years ago; Ordovician from 510 to 439 millions of years ago; Silurian from 439 to 409 millions of years ago; Devonian from 409 to 363 millions of years ago; Carboniferous from 363 to 290 millions of years ago; Permian from 290 to 248 millions of years ago; Triassic from 248 to 210 millions of years ago; Jurassic from 210 to 146 millions of years ago; Cretaceous from 146 to 65 millions of years ago; Tertiary from 65 to 1.64 millions of years ago; Quaternary from 1.64 millions of years ago. The period from Cambian to Permian represents Paleozoic era (Marine life dominated; life spread to land in the mid-Paleozoic); the period from Triassic to Cretaceous represents Mesozoic era (Age of Dinosaurs); and the periods after tertiary represents Cenozoic era (Modern era). The five mass extinctions labeled on the timescale are as follows: 439 millions of years ago: Ordovician extinction: 85 percent of all marine species lost, the predominant life forms at that time. 363 millions of years ago: Devonian extinction: 80 percent of marine species lost; end of the “Age of Fishes.” 248 millions of years ago: Permian extinction: Largest extinction event on record; 90 to 95 percent of all species lost. 210 millions of years ago: Triassic extinction: more than 75 percent of species lost, many from terrestrial niches; allowed dinosaurs to emerge as the dominant land animals. 65 millions of years ago: Cretaceous extinction: more than 75 percent of species lost, including dinosaurs; “Age of Mammals” begins.

Why do we see mass extinction events occurring at transitions from one

geologic time period to the next?

Earth’s past mass extinctions were due to catastrophic events or physical changes to the atmosphere or oceans, which altered the environment faster than species’ ability to adapt. Though most species loss wasn’t overnight, taking from hundreds to millions of years to unfold, these kinds of events eventually led to the emergence of new species as surviving populations adapted to the available niches (a process that took millions of years). Cycles of extinction and evolution ultimately gave rise to the diversity of life we see on Earth today — estimates range from 3 to 100 million species.

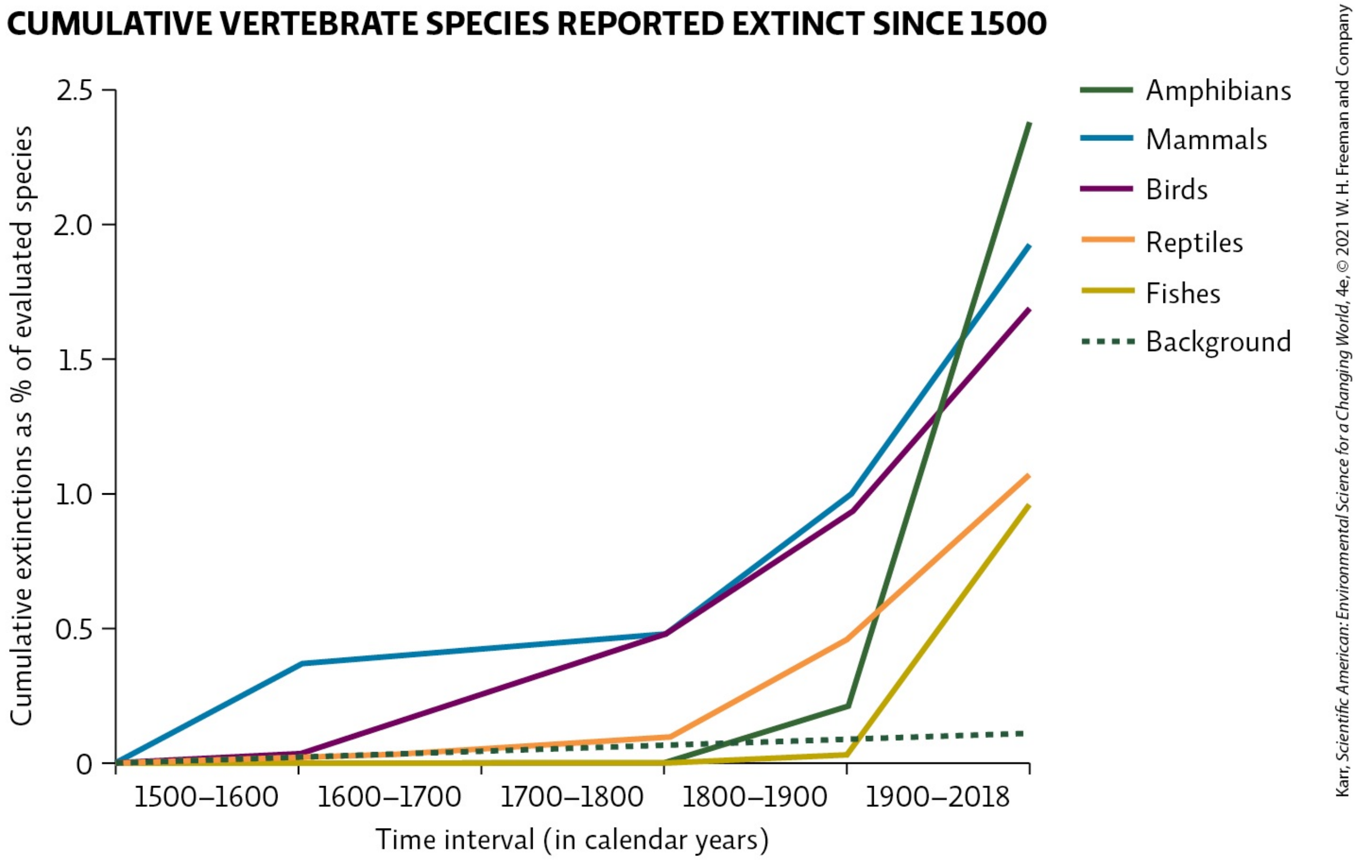
Throughout most of Earth’s history, the *background rate of extinction* — the average rate of extinction that occurs between mass extinction events — has been slow. The fossil record tells us that, on average, 1 or 2 species out of every 1 million species goes extinct each year. In a world with 3 million species, this would be 3 to 6 species per year; if Earth is home to 100 million species, that would be 100 to 200 species per year.

background rate of extinction
: The average rate of extinction that occurred before the appearance of humans or that occurs between mass extinction events.

A 2015 study led by Gerardo Ceballos compared the number of vertebrate species extinctions that have been documented since the year 1500 to what would have been expected if extinction had occurred at a background rate that was determined by an extensive examination of the mammalian fossil record. The data revealed a sharp increase in the number of extinctions beginning about 200 years ago. At background rates, Earth should have seen 9 vertebrate extinctions since 1900; 477 have occurred — that’s 53 times higher than expected.

INFOGRAPHIC 7B THE RATE OF EXTINCTION IS ACCELERATING

Recent rates of species extinctions are well above that expected by the background rate, a trend attributed to human impact such as habitat destruction, the introduction of invasive species, and climate change. This graph, based on analysis techniques developed by Ceballos, shows estimate of extinctions since the year 1500 for vertebrates in comparison to the background rate of extinction. Accelerated extinction rates are seen for vertebrates, especially since the 19th century.



The horizontal axis represents time interval (in calendar years) and is labeled 1500 to 1600, 1600 to 1700, 1700 to 1800, 1800 to 1900, and 1900 to 2018. The vertical axis represents cumulative extinctions as percent of evaluated species and ranges from 0 to 2.5. in increments of 0.5. The positive curve for Amphibians travels along the horizontal axis until 1800 where it increases to 0.2 percent at 1900 and then ends at 2.4 percent at 2018. The positive curve for Mammals starts at the origin, rise to 0.4 percent at 1600, gradually increases to 0.45 percent at 1800, then increase to 1.0 percent at 1900, and then ends at 1.8 percent at 2018. The positive curve for Birds travels along the horizontal axis to 1600 where it increases to 0.45 percent in 1800, then to 0.9 percent in 1900, and the ends at 1.7 percent in 2018. The positive curve for Reptiles starts at the origin and gradually increases to 0.1 percent in 1800, and then ends at 1.0 percent in 2018. The positive curve for Fishes travels along the horizontal axis to 1800 where it rises very slightly to 0.02 percent in 1900, then rapidly rises to end at 0.9 percent in 2018. The positive dashed line for background starts at the origin and gradually rises to 0.1 percent in 2018. All data are approximate.

We have more data on bird and mammal extinctions than those for fish, amphibians, and reptiles. Why do you think this is true? Do you think more data would reveal higher or lower rates of extinction for these groups?

Unfortunately, it’s not just vertebrates that are in trouble — many invertebrate groups appear to be declining at precipitous rates. Scientists are particularly concerned at the decline of insect species. Insects, the largest species group by far, are crucial to ecosystem function, providing services such as pollination, matter recycling, and population control. “What we’re losing is not just the *diversity* part of biodiversity, but the *bio* part: life in sheer quantity,” wrote Brooke Jarvis in a recent *New York Times* article.

In the most comprehensive evaluation of biodiversity ever completed, a 2019 global assessment by the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services estimates 25% of evaluated plant and animal species are threatened; some face imminent extinction without immediate action. Extrapolating from this to include all groups, the authors estimate that 1 million species are at risk. The current rate of extinction is estimated to be 100 to 1,000 times higher than the background rate, and this rate is accelerating.

Most scientists agree that the accelerated extinction we are witnessing can be considered a sixth major extinction event, and that it is largely driven by human actions. As our use of resources increases, driven by population growth and affluence, our impact is becoming much more devastating for other species. We remove the resources they need to survive, minimize their habitat ranges, harvest them at unsustainable rates, introduce new predators or competitors, and strip them of their genetic diversity, all of which slowly eliminate them. British researchers Ian Owens and Peter Bennett analyzed the extinction risk for 1,012 *threatened* bird species (those at risk for becoming endangered) and found that habitat destruction was cited as a risk factor in 70% of the cases. Other human interventions, such as the introduction of non-native species or overharvesting, were implicated in 35% of the cases. (See Module 3.2 for more on species endangerment.)

Some might wonder why scientists are so concerned about species extinctions — after all, extinction is a natural event. But it’s the pace of extinctions that is concerning. Our changes to the environment can be so rapid or so great that natural selection simply cannot keep up — perhaps because a new needed trait is not present in the population, or it cannot spread quickly enough to prevent a population collapse. Module 3.2 will examine the value of biodiversity and why its loss can threaten us all. Indeed, an understanding of how populations evolve, and how we can affect that process, can help us avoid actions that create problems such as the emergence of antibiotic-resistant bacteria or untimely species extinctions.

In Guam, the near-total disappearance of birds between the 1960s and 1980s was a biological murder mystery. The brown tree snake was the cause of their demise, but the inadvertent introduction of this species by humans puts the blame squarely on us.

Efforts to control the brown tree snake on Guam are ongoing and aggressive; as many as

15,000 snakes are captured annually. Control methods include baited traps, canine tracking teams, and toxic “mouse-drops”; there are even rapid response teams that are deployed when a snake sighting is reported on a nearby island. The goal is not to eradicate the snakes (which probably isn’t possible) but to control and contain them so that they don’t find their way to other islands, explains Diane Vice, a wildlife biologist with the Guam Department of Agriculture. “The hope is to create safe habitat,” Vice says, “so that these beautiful native species can once again thrive.”

Select References:

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Hoekstra, H. E., et al. (2005). Local adaptation in the rock pocket mouse (*Chaetodipus intermedius*): Natural selection and phylogenetic history of populations. *Heredity, 94*(2), 217–228.

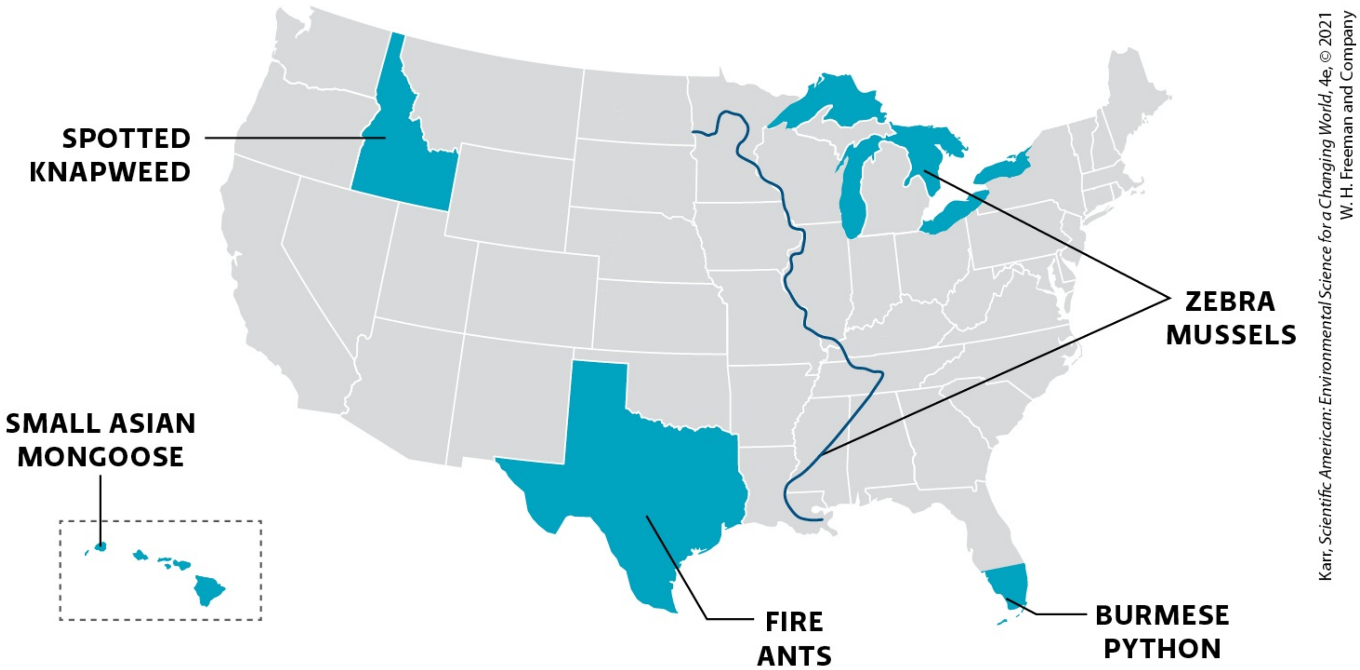
Rogers, H. S., et al. (2017). Effects of an invasive predator cascade to plants via mutualism disruption. *Nature Communications, 8*, 14557.

Savidge, J. A. (1987). Extinction of an island forest avifauna by an introduced snake. *Ecology, 68*(3), 660–668.

End of Module Resources

GLOBAL CASE STUDIES

INVASIVE SPECIES



> Non-native species that find their way to other ecosystems can wreak havoc on native species unprepared to deal with them. Here are a few notable invasive species that are taking their toll on U.S. ecosystems.

The data from the U.S. map shows Spotted Knapweed in Idaho; Fire ants in Texas; Burmese python in the southern tip of Florida; Zebra mussels in the Great Lakes and the Mississippi river; and Small Asian mongoose in Hawaii.

BRING IT HOME

PERSONAL CHOICES THAT HELP

The astonishing variety of life found on Earth is a result of natural selection favoring those individuals within populations that are best able to survive in their particular environment. Given enough time, some populations may be able to adapt to environmental changes. However, human activities may disrupt natural ecosystems so that organisms cannot adapt fast enough to survive, and those organisms may go extinct. Conservation actions can help protect vulnerable organisms and ecosystems.

Individual Steps

- When buying a home, consider an older established area of your community or a location close to work. Suburban sprawl reduces habitat for wildlife, and reliance on cars causes greenhouse gas emissions that contribute to species-threatening climate change.

- Save your pocket change and, at the end of every year, donate the money to a land, marine, or wildlife protection agency.

- Create a personal blog that includes photographs of wildlife, facts about current threats to plants and animals, and articles about conservation.

Group Action

- Throw a party in support of wildlife conservation. Take a collection at the door and donate the money to an organization that supports conservation.

- "Adopt an Organism." The U.S. Fish and Wildlife Service maintains a database of endangered plants and animals in every state. Research this database to find wildlife that interests you. Determine what agency, conservation group, or legislator you could contact and then start your own protection campaign. See what meetings, petitions, and legislation could impact your organism and get involved.

JOEL SARTORE/National Geographic Creative

REVISIT THE CONCEPTS

- Evolutionary biology helps us understand the diversity of life on Earth and how populations change over time. In response to selective pressures that favor the survival or reproductive success of some individuals over others due to inherited traits that better equip them to handle the challenge at hand, populations can adapt to a changing environment — a process known as natural selection.
- Genetic diversity in a population is the raw material on which natural selection operates. A population is said to have evolved if the frequency of genes in a descendant population is different from that in its ancestral population.
- Species can become highly adapted to each other when each is the selective pressure for the other (coevolution). Problems can emerge when species that did not coevolve together meet. For example, a non-native predator may be well adapted to prey on native species in its new habitat but if those native species never coevolved with a similar predator, they may not be able to survive predation.
- Along with natural selection, random events such as genetic drift, the bottleneck effect, and the founder effect also influence the evolution of a population.
- Humans, too, can direct the evolution of a population via artificial selection by breeding individuals with the traits we desire, as in the development of animal breeds or plant varieties.
- In general, the pace of evolution is slow. When extinctions unfold over long periods of time, community connections are not broken because better-adapted species replace their predecessors and the niche remains filled; rapid extinction events may eliminate well-adapted species and break important community connections.
- There have been five mass extinction events in Earth’s past, caused by natural events; today we are experiencing a sixth mass extinction, caused by human impact, that could have devastating consequences for ecosystems and the people who depend on them.

ENVIRONMENTAL LITERACY Understanding the Issue

1 What is biological evolution, and how do populations adapt to changes via natural selection?

1. A butterfly population adapts to a warming environment — explain how this could happen via natural selection.
2. Use the example of a bird population that most commonly feeds on medium-sized insects to distinguish between *stabilizing, directional,* and *disruptive selection*.

3. Explain this statement: Individuals are selected but populations evolve.

2 Why is genetic diversity important to natural selection?

4. As the amount of genetic diversity in a population increases, how does this affect the likelihood that the population will be able to adapt to environmental changes?
5. Does the presence of genetic diversity in a population guarantee it will be able to adapt to changes? Explain.
6. Using the example of the rock pocket mouse, explain the importance of genetic diversity to a population.

3 What is coevolution, and what problems can emerge when species that did not coevolve together suddenly share a habitat?

7. Use the concept of coevolution to explain why the brown tree snake is a much more devastating predator on Guam than it is in its native habitat.
8. Suppose a native Guam bird species began to show evasive behaviors that allowed it to avoid the brown tree snake. Describe a potential coevolution scenario that might have allowed this adaptation to eventually predominate in the population.

4 How do random events influence the evolution of a population?

9. Why is genetic drift considered random whereas natural selection is considered nonrandom?
10. Why might a population, isolated by the founder effect, be more vulnerable to extinction than the original population from which it came?

5 How do humans, intentionally or accidentally, affect the evolution of a population?

11. Give some examples of artificial selection by humans that have been beneficial to human society.
12. Explain how pesticide resistance might evolve in an insect pest.
13. Suppose you wanted to use artificial selection to produce a breed of hairless dogs for people who are allergic to dog hair. How would you go about doing this?

6 What factors affect the pace of evolution and extinction, and why are extinctions that occur quickly more of a concern than those that take a long time to unfold?

14. What factors influence the pace of evolution in the absence of a mass extinction event?

15. Why are *K*-selected species more vulnerable to extinction than *r*-selected species?

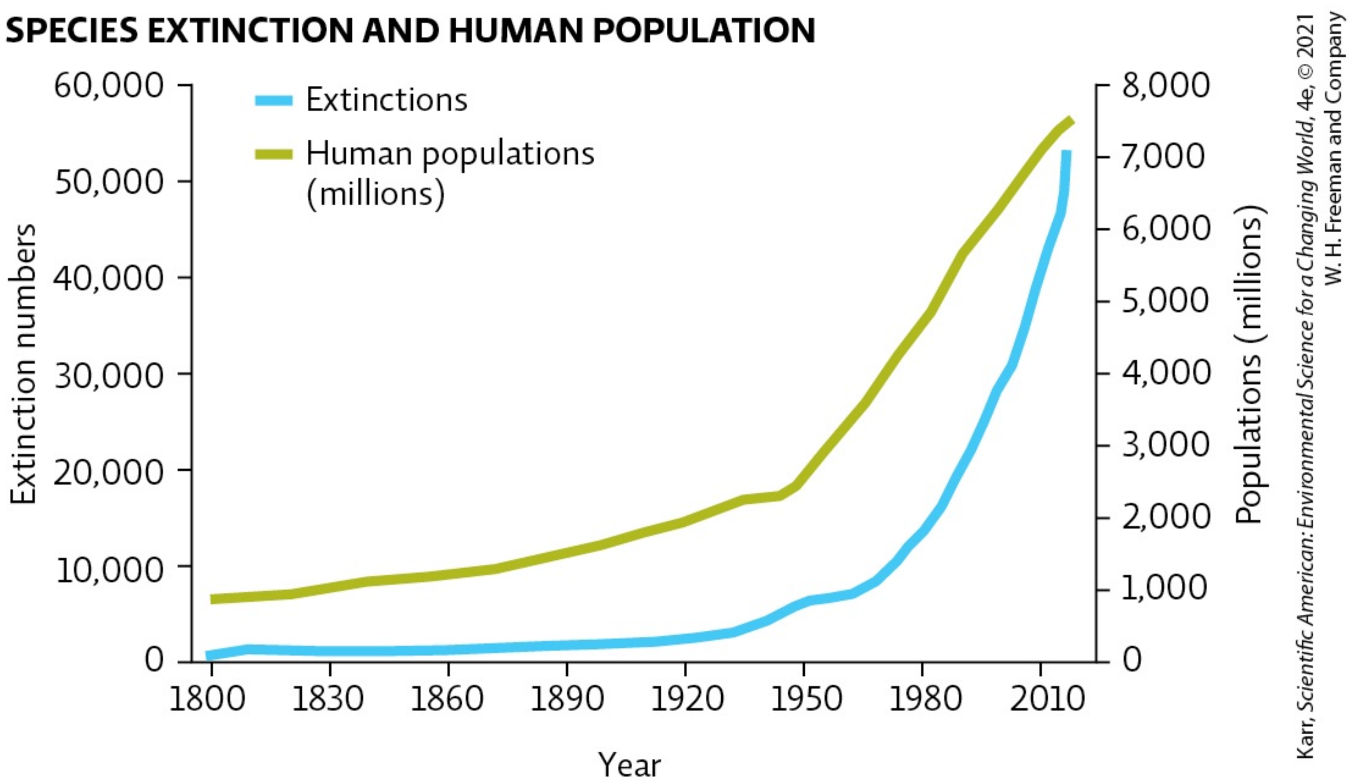
7 How do the mass extinction events of the past compare to extinctions during intervening times and today?

16. Why do most scientists think that we are in the midst of a sixth mass extinction?

17. Why are the changes being imposed by humans difficult for species to adjust to?

SCIENCE LITERACY Working with Data

The following graph depicts the relationship between numbers of extinctions and human population size since the 19th century.



The horizontal axis represents year and ranges from 1800 to 2010, in increments of 30 years. The left vertical axis represents extinction numbers and ranges from 0 to 60,000, in increments of 10,000; the right vertical axis represents populations (in millions) and ranges from 1,000 to 8,000, in increments of 1,000. The positive curve representing extinction starts from (0, 1800), rises slightly till (5,000, 1965), and rises tremendously to end at (52,000, 2010). The positive curve representing population size starts from (1,000, 1800), rises slightly till (2,500, 1950), and rises tremendously to end at (7,500, 2010). All data are approximate.

Interpretation

1. Describe what is happening to:

    a. the extinction rate over time.

    b. human population growth over time.

2. Around what point in time do we see a change in the rate of species extinctions?

3. The two curves have been graphed together. What is the implication of presenting these data in this manner?

Advance Your Thinking

4. The *y* axis is labeled "Extinction numbers." What taxonomic units are being measured? What if the taxonomic unit being evaluated here had been genus (a taxonomic group that can contain more than one species) or family (a taxonomic group that can contain more than one genus)? Would you be more or less concerned about the trend of extinctions? Explain.

5. What type of relationship is suggested by the figure: correlational or causal? What additional data would you like to see to support the graph's main point?

INFORMATION LITERACY Evaluating Information

Life on Earth as we know it is a result of millions of years of evolutionary processes. By most accounts, we are currently witnessing a mass extinction event at our own hands, one that will result in changes in biodiversity, which will necessarily affect life on Earth, including humans.

Investigate this Problem

1. Visit the website of the Center for Biological Diversity at www.biologicaldiversity.org and search the website for information using the key words *extinction crisis*. Read a few articles and then select one article about extinction to evaluate. Identify it (title, author and date [if provided], and URL) and then answer the questions that follow.

Evaluate the Article

2. In your own words, summarize the main point(s) or position of the article you are evaluating.

a. Identify three claims made in the article. (If there are not three claims in the article you chose, chose a different one to evaluate.)

b. Identify the evidence presented to back up each claim and evaluate that evidence. Is it sufficient? (If no evidence is given, where might you go to find that evidence?)

c. Are references given for the evidence? Explain.

Evaluate the Organization

3. Determine if this a reliable information source:

   a. Does the organization have a clear and transparent agenda? Explain.

   b. Who runs this website? Do the credentials of the staff make this source reliable/unreliable? Explain.

Dig Deeper

4. Go to the International Union for Conservation of Nature (IUCN) website (www.iucnredlist.org).

   a. Choose five species at random that are identified as vulnerable, endangered, or critically endangered. Read about each species, and list the threats each faces.

   b. Create one master list of all the threats you encountered for your five species, and categorize them as either *human caused* or *caused by natural events*. Which list is longer?

Draw Conclusions

5. Based on your research, does human impact play a role in the endangerment of species? What actions would be most useful to address these threats? Do you think these actions should be pursued? Support your conclusions with evidence from your research.

Additional study questions are available at Achieve.macmillanlearning.com.

Achieve