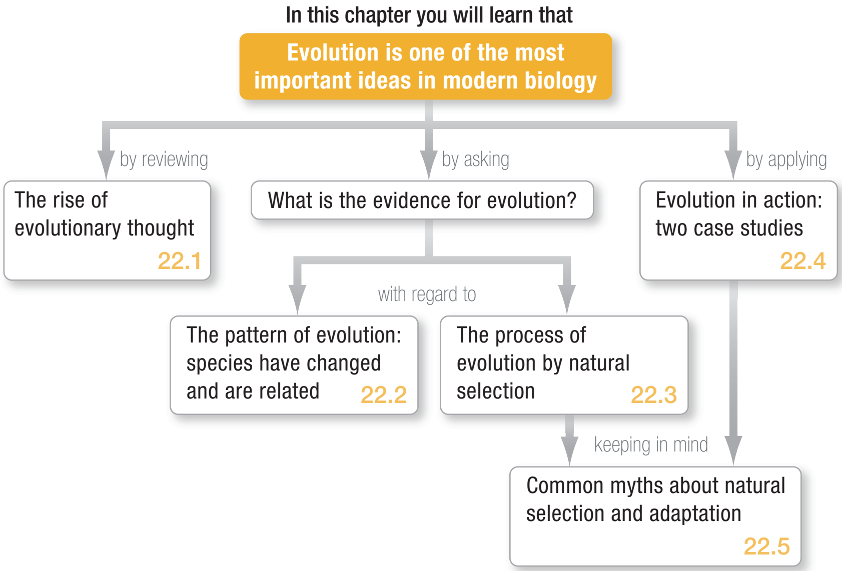
22 Evolution by Natural Selection

Natural selection explains how populations become well suited to their environments over time. The shape and coloration of leafy sea dragons (a fish closely related to seahorses) are heritable traits that help them to hide from predators.



This chapter is about one of the great ideas in science: the theory of evolution by natural selection, formulated independently by Charles Darwin and Alfred Russel Wallace. The theory explains how **populations**—individuals of the same species that live in the same area at the same time—have come to be adapted to environments ranging from arctic tundra to tropical wet forest. It revealed one of the five key attributes of life: Populations of organisms evolve. In other words, the heritable characteristics of populations change over time (Chapter 1).

Evolution by natural selection is one of the best supported and most important theories in the history of scientific research. But like most scientific breakthroughs, this one did not come easily. When Darwin

BIG PICTURE

This chapter is part of the Big Picture. See how on pages 516–517.

published his theory in 1859 in a book called *On the Origin of Species by Means of Natural Selection*, it unleashed a firestorm of protest throughout Europe. At that time, the leading explanation for the diversity of organisms was an idea called special creation.

Special creation held that **(1)** all species are independent, in the sense of being unrelated to each other; **(2)** life on Earth is young—perhaps just 6000 years old; and **(3)** species are immutable, or incapable of change. These beliefs were explained by the instantaneous and independent creation of living organisms by a supernatural being.

Darwin's theory was radically different. How did it differ? In everyday English, the word "theory" suggests a thoughtful guess, but a scientific theory is an explanation for a broad class of observations that is widely supported by overwhelming evidence. (For help with problematic words, see **BioSkills 17**.) Scientific theories usually have two components: a pattern and a process.

1. The *pattern component* is a statement that summarizes a series of observations about the natural world. The pattern component is about facts—about how things *are* in nature.
2. The *process component* is a mechanism that produces that pattern or set of observations.

This chapter begins with an overview of the development of evolutionary thought, and then examines the pattern and process components of the theory of evolution by natural selection.

22.1 The Rise of Evolutionary Thought

People often describe the theory of evolution by natural selection as revolutionary. Revolutions overturn things—they replace an existing entity with something new and often radically different. A political revolution removes the ruling class or group and replaces it with another. The industrial revolution replaced small shops for manufacturing goods by hand with huge, mechanized assembly lines.

A scientific revolution, in contrast, overturns an existing idea about how nature works and replaces it with a radically different idea. Revolutionary scientific theories include Copernicus's theory of the Sun as the center of our solar system, Newton's laws of motion and theory of gravitation, the germ theory of disease, the theory of plate tectonics, and Einstein's general theory of relativity. These theories are the foundation of modern science.

The advance of the theory of evolution by natural section represented a profound scientific revolution. The idea that Darwin and Wallace overturned—that species were supernaturally, not naturally, created—had dominated thinking about the nature of organisms in Western civilization for over 2000 years.

Plato and Typological Thinking

The Greek philosopher Plato claimed that every organism was an example of a perfect essence, or type, created by God, and that these types were unchanging (**Figure 22.1a**). Plato acknowledged that individuals of a species sometimes varied slightly from one another, but that these were just trivial deviations around a "perfect essence."

Today, philosophers and biologists refer to ideas like this as typological thinking. Typological thinking also occurs in the Bible's book of Genesis and in the creation stories of many other religions, where a divine being creates each type of organism.

Aristotle and the Scale of Nature

Not long after Plato developed his ideas, Aristotle ordered the types of organisms known at the time into a linear scheme called the great chain of being, or scale of nature, where "scale" means a ladder or stairway (**Figure 22.1b**). Aristotle proposed that species were fixed types organized into a sequence based on increased size and complexity. The scale started with minerals and lower plants at the bottom, then rose through higher plants, lower and

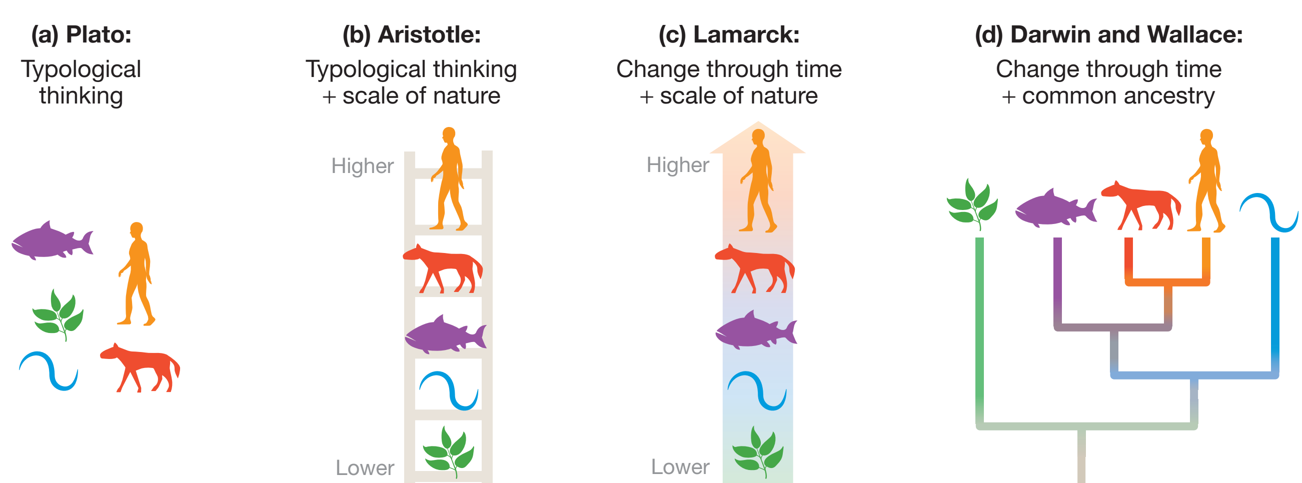


Figure 22.1 Models of the Diversity of Life Have Changed through Time. Visual models are helpful for comparing ideas. The models shown here include only five living species, for simplicity. Each model is explained in the text.

higher invertebrates (animals without backbones), and lower and higher vertebrates (animals with backbones) to humans at the top.

Aristotle's ideas were still popular in scientific and religious circles well into the 1700s. Since many cultures had embraced Aristotle's model for so long—over 20 centuries—the notion of "lower" and "higher" species lingers as a cultural habit, even today (discussed in Section 22.5).

Lamarck and the Idea of Evolution as Change through Time

Typological thinking eventually began to break down. In 1809 the biologist Jean-Baptiste de Lamarck proposed the first formal theory of **evolution**—that species are not static but change through time. However, the pattern component of Lamarck's theory was initially based on the scale of nature.

When he started his work on evolution, Lamarck claimed that simple organisms originate at the base of the scale by spontaneous generation (see Chapter 1) and then evolve by moving up the scale over time (**Figure 22.1c**). Thus, Lamarckian evolution is progressive in the sense of always producing larger and more complex, or "better," species.

Lamarck also contended that species change through time via the inheritance of acquired characters. The idea here is that as an individual develops, its phenotype changes in response to challenges posed by the environment, and it passes on these phenotypic changes to offspring. A classic Lamarckian scenario is that giraffes develop long necks as they stretch to reach leaves high in treetops, and they then produce offspring with elongated necks.

Darwin and Wallace and Evolution by Natural Selection

As his thinking matured, Lamarck eventually abandoned his linear and progressive view of life. Darwin and Wallace concurred. But more important, they emphasized that the process responsible for change through time—evolution—occurs because traits vary among the individuals in a population, and because individuals with certain traits leave more offspring than others do.

Darwin and Wallace's proposal was a radical break from the typological thinking that had dominated scientific thought since Plato. Darwin claimed that instead of being unimportant, variation among individuals in a population was the key to understanding the nature of species. Biologists refer to this view as **population thinking.**

The theory of evolution by natural selection was revolutionary for several reasons:

1. It overturned the idea that species are static and unchanging. Instead, it suggested that species change through time and are related by common ancestry (**Figure 22.1d**).
2. It replaced typological thinking with population thinking.
3. It was scientific. It proposed a mechanism that could account for change through time and made predictions that could be tested through observation and experimentation.

Plato and his followers emphasized the existence of fixed types, whereas evolution by natural selection is all about change and diversity. With the advent of evolutionary thought, new questions arose: What evidence backs the claim that species are not fixed types? What data support the theory of evolution by natural selection?

22.2 The Pattern of Evolution: Have Species Changed, and Are They Related?

In *On the Origin of Species*, Darwin repeatedly described evolution as **descent with modification.** He meant that species that lived in the past are the ancestors of the species existing today, and that species change through time.

This view was a revolutionary departure from the independently created and immutable species embodied in Plato's work and in the idea of special creation. In essence, the pattern component of the theory of evolution by natural selection makes two predictions about the nature of species:

1. Species change through time.
2. Species are related by common ancestry.

Let's consider the evidence for each prediction in turn.

Evidence for Change through Time

When Darwin began his work, biologists and geologists had just begun to assemble and interpret the fossil record. A **fossil** is any trace of an organism that lived in the past. These traces range from bones, branches, shells, and dung to tracks or impressions left by organisms in soft sediments such as sand and clay. The **fossil record** consists of all the fossils that have been found on Earth and described in the scientific literature.

Why did data in the fossil record support the hypothesis that species have changed through time? And what data from **extant species**—those living today—support the claim that they are modified forms of ancestral species?

The Vastness of Geologic Time Evidence for the Earth's vast age began to mount in the late 1700s with James Hutton's proposal of the principle of uniformitarianism—the idea that geological processes occurring today are similar to what occurred in the past. Hutton reached his geological insight by evaluating evidence—he traveled around Europe and measured patterns and rates of rock formation and erosion.

Sedimentary rocks form from sand or mud or other materials deposited in layers at locations such as beaches or river mouths. Hutton calculated that sedimentary rocks form at an extremely slow rate. When he extrapolated this rate to determine how long it would take for massive rock formations to form, it was clear that Earth was very old. It was much, much older than the 6000 years claimed by proponents of special creation.

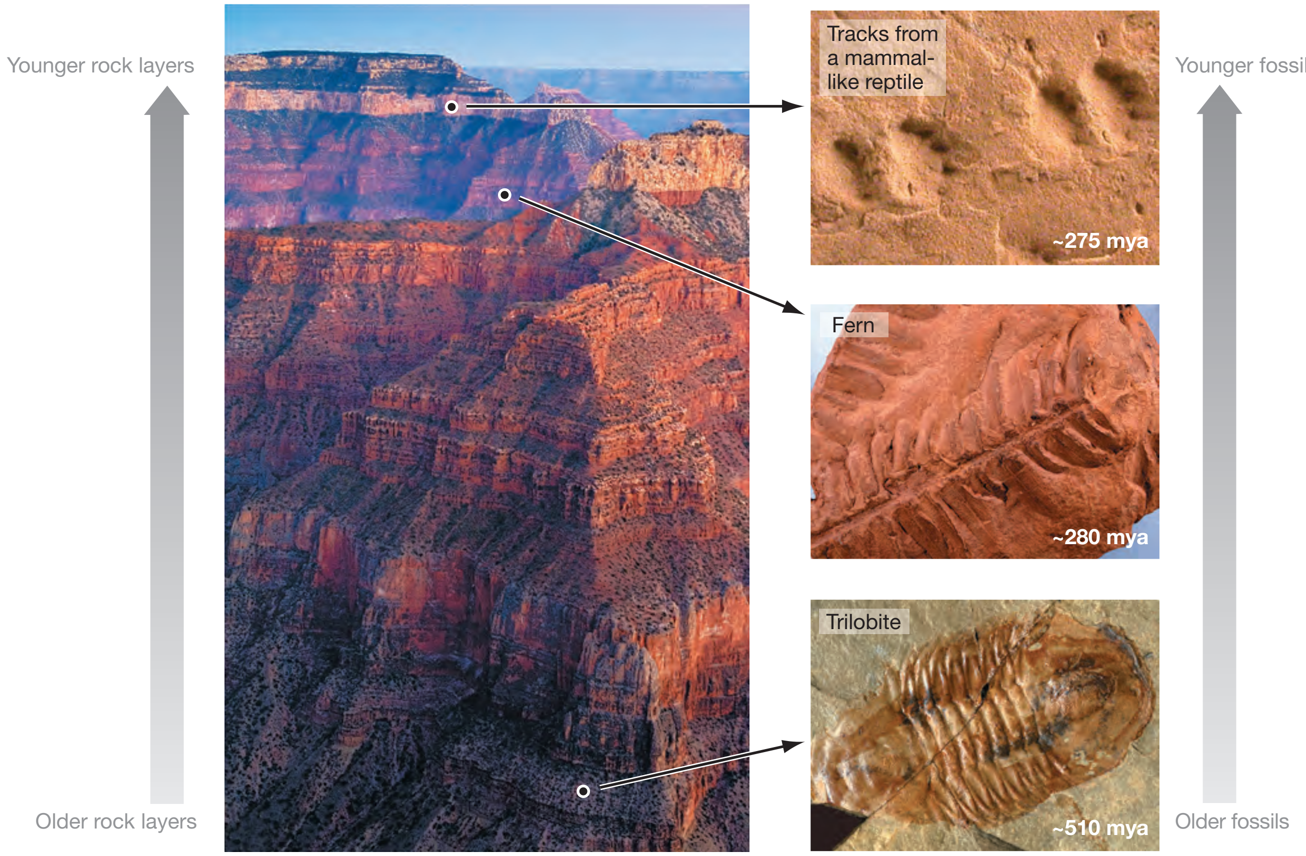


Figure 22.2 Sedimentary Rocks Reveal the Vastness of Geologic Time. The relative ages of sedimentary rocks are used to determine the relative ages of fossil organisms because younger layers are deposited on top of older ones. The deepest rock layer in the Grand Canyon is over a billion years old, and the top layer is 270 million years old.

Hutton's ideas were popularized by Darwin's close friend, the geologist Charles Lyell. Sedimentary rocks, along with rocks derived from episodic lava flows, form with younger layers deposited on top of older layers. Lyell and others used this information to place fossils in a younger-to-older sequence, based on the fossils' relative position in layers of sedimentary rock (**Figure 22.2**).

As the scientists observed similarities in rocks and fossils at different sites, they began to create a **geologic time scale:** a sequence of named intervals called eons, eras, and periods that represented the major events in Earth history (see Chapter 25). The geologic time scale was a relative one, however. The absolute age of Earth was still unknown.

After Marie Curie's discovery of radioactivity in the late 1800s, researchers realized that radioactive decay—the steady rate at which unstable "parent" atoms are converted into more stable "daughter" atoms—furnished a way to assign *absolute* ages, in years, to the relative ages in the geologic time scale. Radioactive decay functions as a "natural clock." For example, the half-life of uranium-238 is about 4.5 billion years, which means that 50 percent of uranium-238 atoms will decay to lead-206 atoms during this time. Knowing the half-life, geologists can use the ratio of uranium to lead in a rock sample to infer the age of the sample.

According to data from radiometric dating, Earth is about 4.6 billion years old, and the earliest signs of life appear in rocks that formed 3.4–3.8 billion years ago. Data from relative and absolute dating techniques agree: Life on Earth is ancient. A great deal of time has gone by for change to occur.

Extinction Changes the Species Present over Time In the early nineteenth century, researchers began discovering fossil bones, leaves, and shells that were unlike structures from any known animal or plant. At first, many scientists insisted that living examples of these species would be found in unexplored regions of the globe. But as research continued and the number and diversity of fossil collections grew, the argument became less and less plausible.

The issue was finally settled in 1812 when Baron Georges Cuvier published a detailed analysis of several **extinct species**—that is, species that no longer exist. Cuvier intentionally focused on the fossils of large terrestrial animals such as mammoths, mastodons, giant armadillos, giant deer, and giant sloths. Unlike many plants or marine animals, he reasoned, it is very unlikely that large, distinctive terrestrial animals such as these would remain undiscovered if they were still alive (**Figure 22.3**). Cuvier's overwhelming evidence convinced scientists of the fact of extinction.

Darwin interpreted extinct forms as evidence that species are not static, immutable entities, unchanged since the moment of special creation. He reasoned that if species have gone extinct, then the array of species living on Earth has changed through time.

Figure 22.3 Evidence of Extinction. This 19th century drawing depicts Cuvier's fossil evidence. Scientists agreed that the sloth, like other giant fossil vertebrates, was too large and unique to be overlooked if it were alive; it must have gone extinct.

Recent analyses of the fossil record suggest that over 99 percent of all the species that have ever lived are now extinct. The data also indicate that species have gone extinct continuously throughout Earth's history—not just in one or even a few catastrophic events (see Chapter 25).

Transitional Features Link Older and Younger Species Long before Darwin published his theory, researchers reported striking resemblances between the fossils found in the rocks underlying certain regions and the living species succeeding them in the same geographic areas, such as the extinct giant sloths of South America and the sloths that occur there today. The pattern was so widespread that it became known as the "law of succession."

Darwin pointed out that this pattern provided strong evidence in favor of the hypothesis that species had changed through time. He proposed that the extinct forms and living forms were related—that they represented ancestors and descendants.

As the fossil record expanded, researchers discovered species with characteristics that broadened the scope of the law of succession. A **transitional feature** is a trait in a fossil species that is intermediate between those of ancestral (older) and derived (younger) species. For example, intensive work over the past several decades has yielded fossils that document a gradual change over time from aquatic animals that had fins to terrestrial animals that had limbs

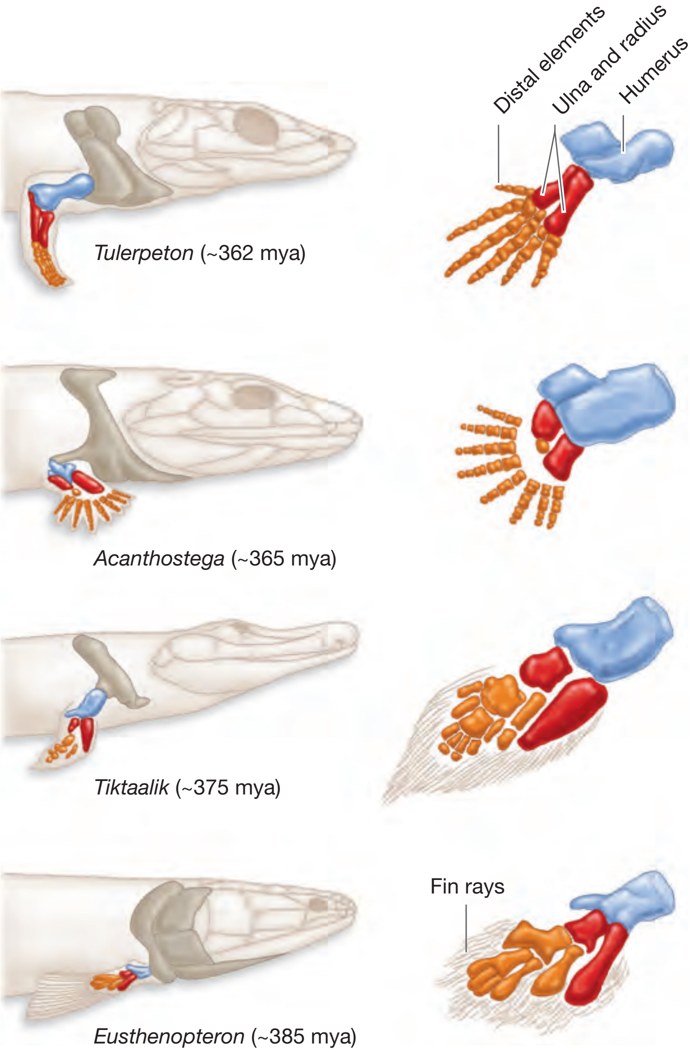


Figure 22.4 Transitional Features during the Evolution of the Tetrapod Limb. Fossil species similar to today's lungfish and tetrapods have fin and limb bones that are transitional features. *Eusthenopteron* was aquatic; *Tulerpeton* was probably semiaquatic (mya = million years ago).

✔ Contrast how the transitions shown above would fit into Lamarck's early model of evolution (Figure 22.1c) versus Darwin and Wallace's model of evolution (Figure 22.1d).

(see **Figure 22.4**). Over a period of about 25 million years, the fins of species similar to today's lungfish transitioned into limbs similar to those found in today's amphibians, reptiles, and mammals—a group called the tetrapods (literally, "four-footed").

These observations support the hypothesis that an ancestral lungfish-like species first used stout, lobed fins to navigate in shallow aquatic habitats. Then, over many generations, some individuals acquired traits that allowed them to move onto land. Their descendants (who inherited these traits) further evolved, becoming more and more like today's tetrapods in appearance and lifestyle. Note that such evolutionary transitions are not goal oriented or purposeful. Rather, some individuals with favorable traits managed to survive and reproduce in the new environment, resulting in change in the population over time (explained further in Section 22.3).

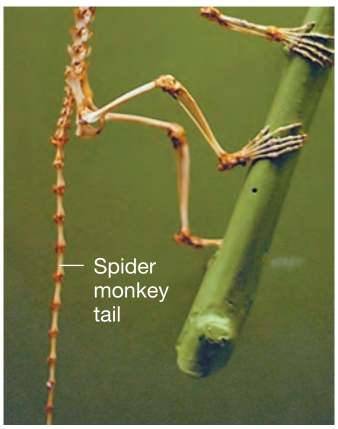
Similar sequences of transitional features document changes that led to the evolution of feathers and flight in birds; stomata and vascular tissue in plants; upright posture, flattened faces, and large brains in humans; jaws in vertebrates; the loss of limbs in snakes; and other traits. Data like these are consistent with predictions from the theory of evolution: If the traits observed in more recent species evolved from traits in more ancient species, then transitional forms are expected to occur in the appropriate time sequence. Note, however, that individual fossils of transitional forms are not necessarily *direct* ancestors of later species—they may be relatives of the direct ancestor.

The fossil record provides compelling evidence that species have evolved. What data from extant forms support the hypothesis that the characteristics of species change through time?

Vestigial Traits Are Evidence of Change through Time Darwin was the first to provide a widely accepted interpretation of vestigial traits. A **vestigial trait** is a reduced or incompletely developed structure that has no function, or reduced function, but is clearly similar to functioning organs or structures in ancestral species or closely related species.

Biologists have documented thousands of examples of vestigial traits.

- Some whales and snakes have tiny hip and leg bones that do not help them swim or slither.
- Ostriches and kiwis have reduced wings and cannot fly.
- Eyeless, blind cave-dwelling fish have eye sockets.
- Monkeys and many other primates have long tails; but our tiny tailbone, or coccyx, illustrated in Figure 22.5, is too small to help us maintain balance or grab tree limbs for support.
- Many mammals, including primates, are able to erect their hair when they are cold or excited. This behavior manifests itself as goose bumps in humans, but goose bumps are largely ineffective in warming us or signaling our emotional state.



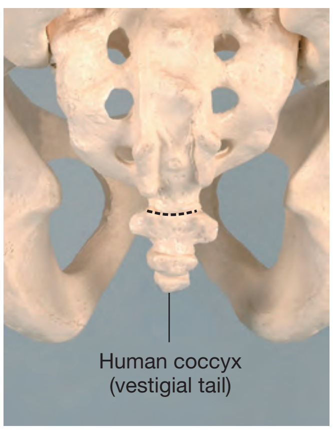


Figure 22.5 Vestigial Traits Are Reduced Versions of Traits in Other Species. The tailbone is a human trait that has reduced function. It is no longer useful for balance and locomotion.

✔ How could vestigial traits such as the tiny human tailbone be explained via inheritance of acquired characters?

The existence of vestigial traits is inconsistent with the idea of special creation, which maintains that species were perfectly designed by a supernatural being and that the characteristics of species are static. Instead, vestigial traits are evidence that the characteristics of species have changed over time.

The change in species over time is logical because the environments of species change dramatically over time. Change can occur due to abiotic factors, such as a rise in temperature or a drop in sea level (see Chapter 49), and biotic factors, such as arrival of a new parasite or the extinction of a predator (see Chapter 52). For example, a tail can be a beneficial, heritable trait for life in the forest canopy, but it is less beneficial as the forest transitions to grassland due to changes in rainfall patterns.

Current Examples of Change through Time Biologists have documented hundreds of contemporary populations that are evolving in response to changes in their environment. Bacteria have evolved resistance to drugs. Weedy plants have evolved resistance to herbicides, and insect pests of crops have evolved resistance to pesticides. The timing of bird migrations and the blooming of flowering plants have evolved in response to ongoing climate change. Native species have evolved in response to the introduction of invasive species. Section 22.4 provides a detailed analysis of research on two examples of evolution in action. Section 22.5 explains that these changes were not purpose-driven.

To summarize, change through time continues and can be measured directly. Evidence from the fossil record and living species indicates that life is ancient and that species have changed through the course of Earth's history.

Evidence of Descent from a Common Ancestor

Data from the fossil record and contemporary species refute the idea that species are static, unchanging types. What about the claim that species were created independently—meaning that they are unrelated to each other?

Similar Species Are Found in the Same Geographic Area Charles Darwin began to realize that species are related by common ancestry during a five-year voyage he took aboard the English naval ship HMS *Beagle*. While fulfilling its mission to explore and map the coast of South America, the *Beagle* spent a few weeks in the Galápagos Islands off the coast of present-day Ecuador. Darwin had taken over the role of ship's naturalist and, as the first scientist to study the area, gathered extensive collections of the plants and animals found in these islands. Most famous among the birds he collected were the Galápagos finches (featured in Section 22.4) and the Galápagos mockingbirds, pictured in Figure 22.6a.

Several years after Darwin returned to England, a colleague pointed out that the mockingbirds collected from some of the different islands were distinct species, based on differences in coloration and beak size and shape. This struck Darwin as remarkable. Why would species that inhabit neighboring islands be so similar, yet clearly distinct? This turns out to be a widespread pattern: In island groups across the globe, it is routine to find similar but distinct species on neighboring islands.

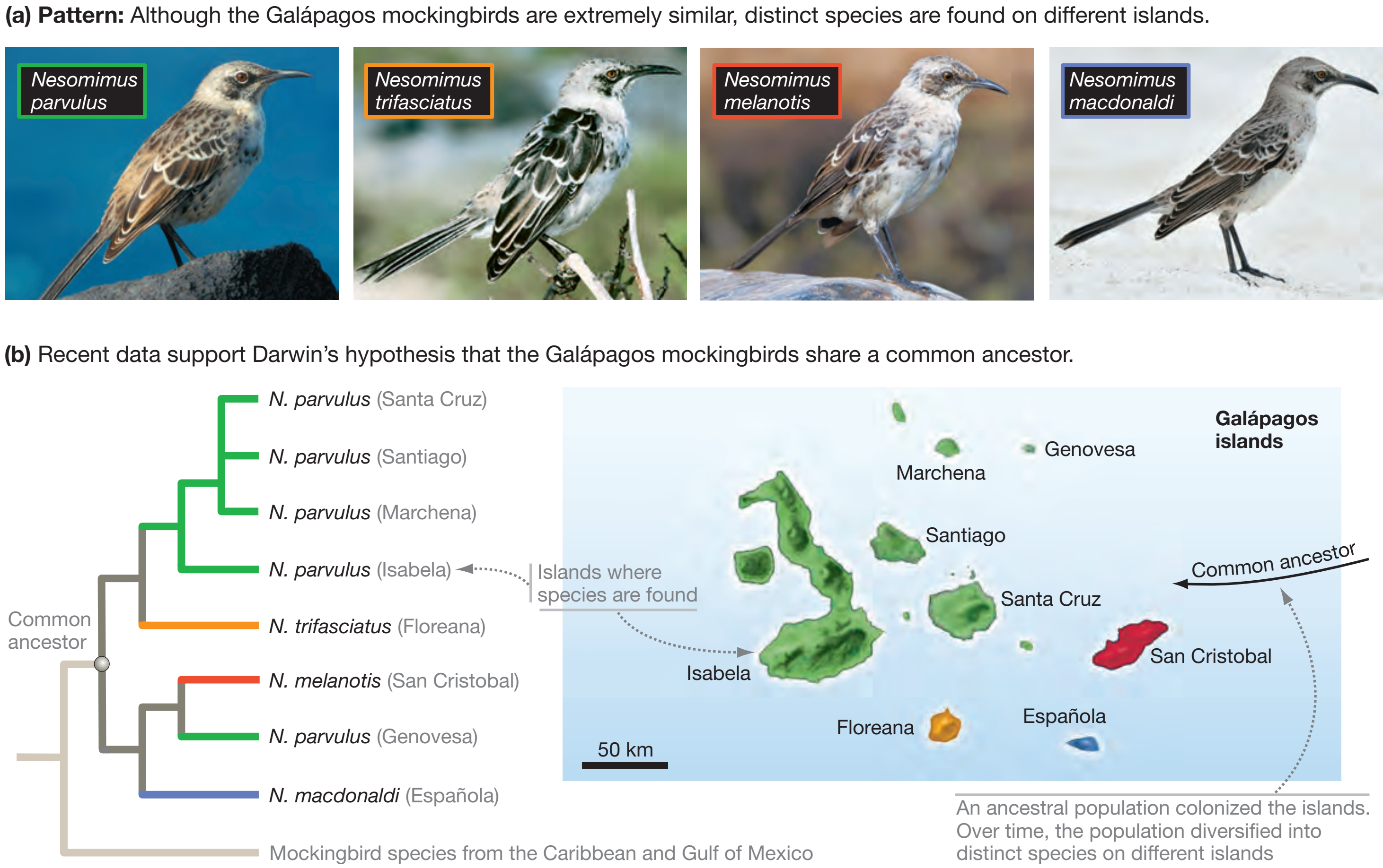


Figure 22.6 Close Relationships among Island Forms Argue for Shared Ancestry.

Darwin realized that this pattern—puzzling when examined as a product of special creation—made perfect sense when interpreted in the context of evolution, or descent with modification. The mockingbirds were similar, he proposed, because they had descended from the same common ancestor. That is, instead of being created independently, mockingbird populations that colonized different islands had changed through time and formed new species (**Figure 22.6b**).

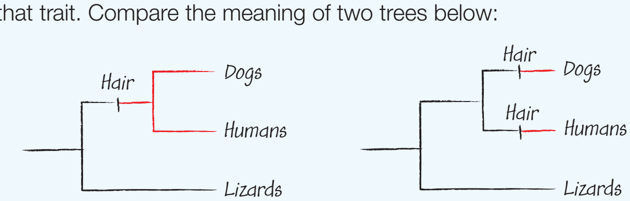
Recent analyses of DNA sequences in these mockingbirds support Darwin's hypothesis. Researchers have used the DNA sequence comparisons to place the mockingbirds on a **phylogenetic tree**—a branching diagram that describes the ancestor–descendant relationships among species or other taxa (see Chapter 25). As Figure 22.6b shows, the Galápagos mockingbirds are each other's closest living relatives. As Darwin predicted, they share a single common ancestor. (For help with reading phylogenetic trees, see **BioSkills 13**.)

Similar Species Share Homologies Translated literally, homology means "the study of likeness." When biologists first began to study the anatomy of humans and other vertebrates, they were struck by the remarkable similarity of their skeletons, muscles, and organs. But because the biologists who did these early studies were advocates of special creation, they could not explain why striking similarities existed among certain organisms but not others.

Today, biologists recognize that **homology** is a similarity that exists in species due to common ancestry. Human hair and dog fur are homologous. Humans have hair and dogs have hair (fur) because they share a common ancestor—an early mammal species—that had hair (see **Making Models 22.1**).

Making Models 22.1 Tips on Drawing Phylogenetic Trees

Phylogenetic trees can help you understand the concept of homology (see **BioSkills 13** and Chapter 25). You can use a tick mark on a branch to symbolize the origin of a new trait. All the organisms to the right of that tick mark are assumed to possess that trait. Compare the meaning of two trees below:

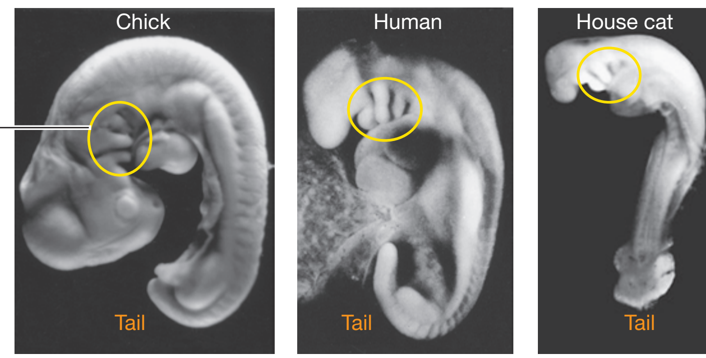
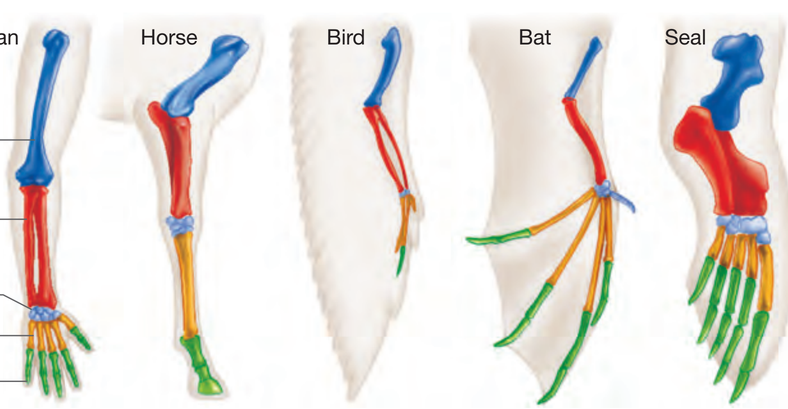


"Hair is homologous in dogs and humans" | "Hair is not homologous in dogs and humans"

MODEL Draw a dot on the node (branching point) of each tree that represents the most recent common ancestor of dogs and humans, and indicate if it had hair. Which tree is correct?

To see this model in action, go to https://goo.gl/TfHLCq

SUMMARY **Table 22.1** Three Levels of Homology

Level	Example
Genetic homology Similarity in DNA, RNA, or amino acid sequences due to inheritance from a common ancestor Amino acid sequences from a portion of the *Aniridia* gene product found in humans are 90 percent identical to those found in the *Drosophila* eyeless gene product.	**Gene:** — **Amino acid sequence (single-letter abbreviations):** *Aniridia* (Human): LQRNRTSFTQEQIEALEKEFERTHYPDVFARERLAAKIDLPEARIQVWFSNRRAKWRREE *eyeless* (Fruit fly): LQRNRTSFTNDQIDSLEKEFERTHYPDVFARERLAGKIGLPEARIQVWFSNRRAKWRREE (For a key to the single-letter abbreviations used for the amino acids, see Figure 3.2.)
Developmental homology Similarity in embryonic form or developmental processes due to inheritance from a common ancestor The early embryonic stages of a chick, a human, and a cat show a strong resemblance and are the product of similar developmental processes.	Pharyngeal pouch 
Structural homology Similarity in adult organismal structures due to inheritance from a common ancestor Even though their function varies, all vertebrate limbs are modifications of the same number and arrangement of bones. (These limbs are not drawn to scale.)	Humerus Radius and ulna Carpals Metacarpals Phalanges 

Homology can be recognized and studied at three levels, summarized in **Table 22.1**:

1. **Genetic homology** occurs in DNA nucleotide sequences, RNA nucleotide sequences, or amino acid sequences. Perhaps the most fundamental of all homologies is the genetic code. With a few minor exceptions, all organisms use the same rules for transferring the information coded in DNA into proteins (see Chapter 16). For example, the *eyeless* gene in fruit flies and the *Aniridia* gene in humans are so similar that their protein products are 90 percent identical in amino acid sequence. Both genes act in determining where eyes will develop—even though fruit flies have a compound eye with many lenses and humans have a camera eye with a single lens.
2. **Developmental homology** is observed in embryos. For example, early chick, human, and cat embryos have tails and structures called pharyngeal pouches that are a product of similar developmental processes. Later, these pouches are lost in all three species, and tails are lost in humans. But in fish, the pharyngeal pouches stay intact and give rise to functioning gills in adults. To explain this observation, biologists hypothesize that pharyngeal pouches and tails exist in chicks, humans, and cats because they existed in the fishlike species that was the common ancestor of today's vertebrates. Pharyngeal pouches are a vestigial trait in chicks, humans, and cats; embryonic tails are a vestigial trait in humans.
3. **Structural homology** is a similarity in adult **morphology**, or form. A classic example is the common structural plan observed in the limbs of vertebrates. In Darwin's own words, "What could be more curious than that the hand of a man, formed for grasping, that of a mole for digging, the leg of the horse, the paddle of the porpoise, and the wing of the bat, should all be constructed on the same pattern, and should

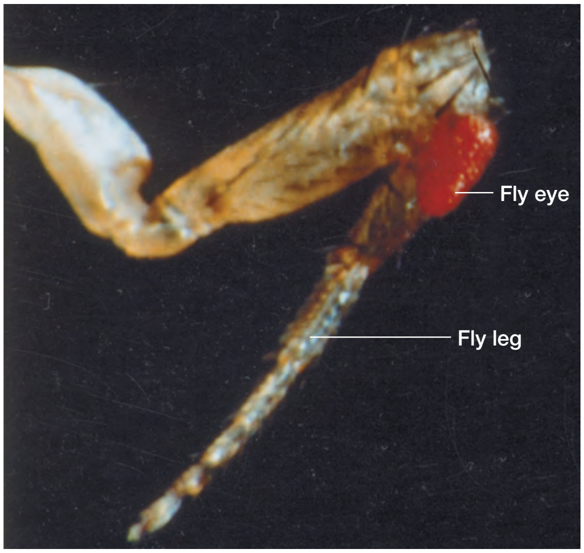


Figure 22.7 Evidence for Homology: A Gene from One Organism Can Be Expressed in Another Organism. A fruit fly eye formed on the leg of a fruit fly where a mouse gene for eye formation had been inserted. The fruit fly "read" the mouse gene as its own.

include the same bones, in the same relative positions?" An engineer would never use the same underlying structure to design a grasping tool, a digging implement, a walking device, a propeller, and a wing. Instead, the structural homology exists because mammals evolved from a lungfish-like ancestor that had the same general arrangement of bones in its fins.

The three levels of homology interact. Genetic homologies cause the developmental homologies observed in embryos, which then lead to the structural homologies recognized in adults.

In some cases, hypotheses about homology can be tested experimentally. For example, researchers **(1)** isolated a mouse gene that was thought to be homologous to the fruit fly *eyeless* gene, **(2)** inserted the mouse gene into fruit fly embryos, **(3)** stimulated expression of the foreign gene in locations that normally give rise to appendages, and **(4)** observed formation of eyes on legs and antennae (Figure 22.7). The function of the inserted gene was identical to that of *eyeless*. This result was strong evidence that the fruit fly and mouse genes are homologous, as predicted from their sequence similarity.

Homology is a key concept in contemporary biology:

- Chemicals that cause cancer in humans can often be identified by testing their effects on mutation rates in bacteria, yeast, zebrafish, mice, and other model organisms because the molecular machinery responsible for copying and repairing DNA is homologous in all organisms (see Chapter 15).
- Drugs intended for human use can be tested on mice or rabbits if the proteins or other gene products targeted by the drugs are homologous.
- Unidentified sequences in the human, rice, or other genomes can be identified if they are homologous to known sequences in yeast, fruit flies, or other well-studied model organisms (see Chapter 20 and BioSkills 11).

The theory of evolution by natural selection predicts that homologies will occur. If species were created independently of one another, as special creation claims, these types of similarities would not occur.

Current Examples of Descent from a Common Ancestor Biologists have documented dozens of contemporary populations that are undergoing speciation—a process that results in one species splitting into two or more descendant species. Some populations have served as particularly well-studied examples of speciation in action, such as populations of fruit flies and sunflowers (see Chapter 24). The contemporary examples of speciation are powerful evidence that species living today are the descendants of species that lived in the past. They support the claim that all organisms are related by descent from a common ancestor.

Evolution's "Internal Consistency"—The Importance of Independent Data Sets

Biologists draw on data from several sources to challenge the hypothesis that species are immutable and were created independently. The data support the idea that species have descended, with modification, from a common ancestor. Table 22.2 summarizes this evidence.

Perhaps the most powerful evidence for any scientific theory, including evolution by natural selection, is what scientists call internal consistency. This is the observation that data from independent sources agree in supporting predictions made by a theory.

As an example, consider the evolution of whales and dolphins—a group called the cetaceans.

- ***The fossil record*** contains a series of species that are clearly identified as cetaceans based on the unusual ear bones found only in this group. Some of the species have the long legs and compact bodies typical of mammals that live primarily on land; some are limbless and have the streamlined bodies typical of aquatic mammals; some have intermediate features.

SUMMARY Table 22.2 Evidence for Evolution

Prediction 1: Species Are Not Static, but Change through Time

- Life on Earth is ancient. The fossil record shows a change in life over time.
- Fossil (extinct) species frequently resemble living species found in the same area.
- Transitional features document change in traits through time.
- Vestigial traits are common.
- The characteristics of populations vary within species and can be observed changing today.

Prediction 2: Species Are Related, Not Independent

- Similar species often live in the same geographic area.
- Homologous traits are common and are recognized at three levels:
  1. genetic (gene structure and the genetic code)
  2. developmental (embryonic structures and processes)
  3. structural (morphological traits in adults)
- The formation of new species, from preexisting species, can be observed today.

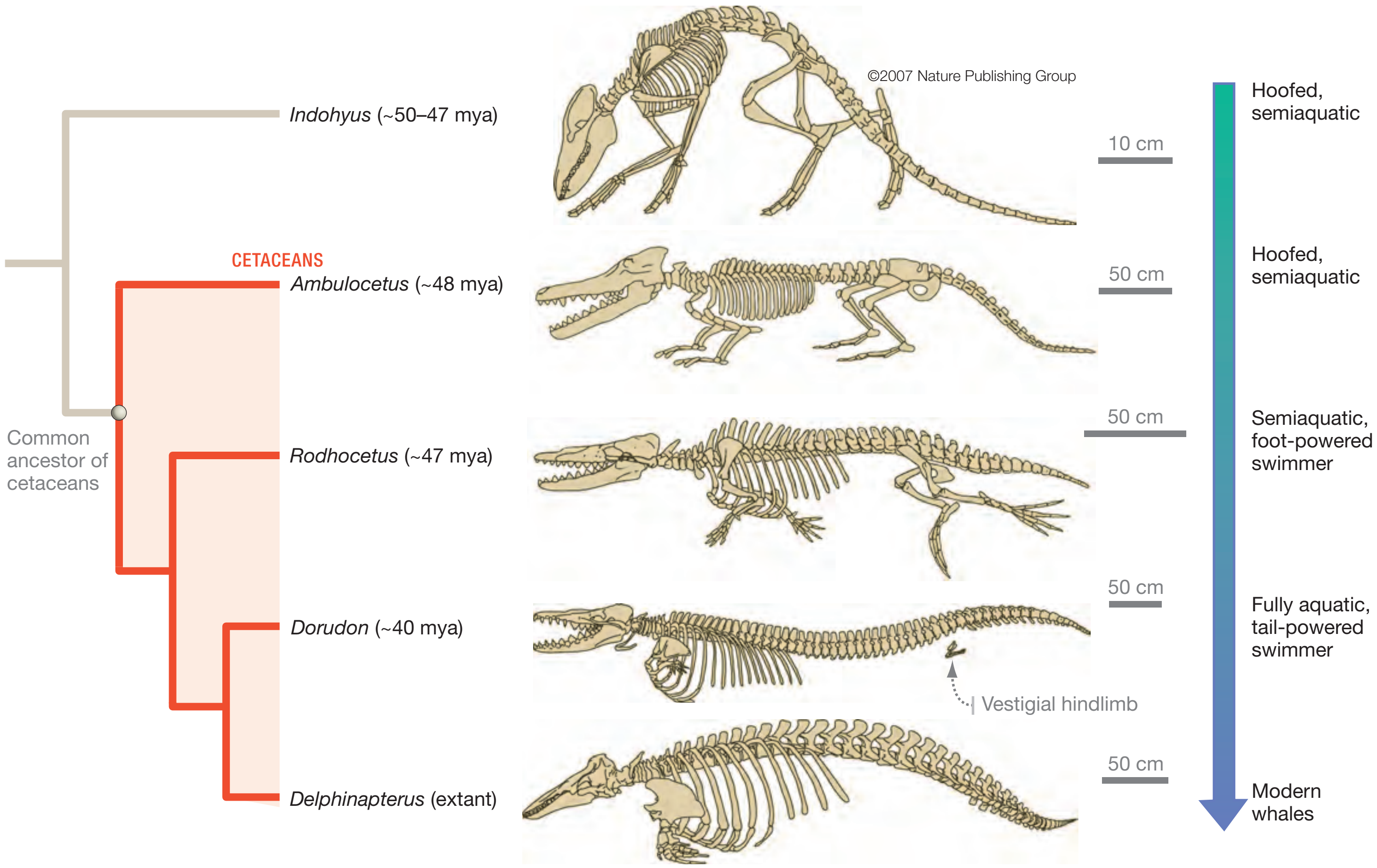


Figure 22.8 Data on Evolution from Independent Sources Are Consistent. This phylogeny of fossil cetaceans is consistent with data from relative dating, absolute dating, and phylogenies estimated from molecular traits in living species—all agree that whales evolved from terrestrial ancestors that also gave rise to hippos.

- ***A phylogeny of the fossil cetaceans,*** estimated on the basis of similarities and differences in morphological traits other than limbs and overall body shape, indicates that a gradual transition occurred between terrestrial forms and aquatic, whale-like forms (Figure 22.8).
- ***Relative dating,*** based on the positions of sedimentary rocks where the fossils were found, agrees with the order of species indicated in the phylogeny.
- ***Absolute dating,*** based on analyses of radioactive atoms in rocks in or near the layers where the fossils were found, also agrees with the order of species indicated in the phylogeny.
- ***A phylogeny of living whales and dolphins,*** estimated from similarities and differences in DNA sequences, indicates that hippos—which spend much of their time in shallow water—are the closest living relative of cetaceans. This observation supports the hypothesis that cetaceans and hippos shared a common ancestor that was semiaquatic.
- ***Vestigial hip and hindlimb bones*** occur in some whales as adults, and vestigial hindlimb buds—outgrowths where legs form in other mammals—occur in some dolphin embryos.

The general message here is that many independent lines of evidence converge on the same conclusion: Whales gradually evolved from a terrestrial ancestor about 50 million years ago.

As you evaluate the evidence supporting the pattern component of the theory of evolution, though, it's important to recognize that no single observation or experiment instantly "proved" the fact of evolution. Rather, data from many different sources are much more consistent with evolution than with special creation. Descent with modification is a successful and powerful scientific theory because it explains observations—such as vestigial traits and the close similarities among species on neighboring islands—that special creation does not.

What about the process component of the theory of evolution by natural selection? If hippos and whales were not created independently, how did they come to be?

CHECK YOUR UNDERSTANDING

If you understand that . . .

- Species are not static, but change through time.
- Species are related by common ancestry.

✔ You should be able to . . .

1. Determine what kind of evidence would support the hypothesis that birds evolved from dinosaurs.
2. Explain why the DNA sequences of chimpanzees and humans are about 96 percent similar.

Answers are available in Appendix A.

22.3 The Process of Evolution: How Does Natural Selection Work?

Darwin's greatest contribution did not lie in recognizing the fact of evolution. Lamarck and other researchers, including Darwin's own grandfather Erasmus Darwin, had proposed evolution long before Charles Darwin began his work. Instead, Darwin's crucial insight lay in recognizing a process, called natural selection, that could explain the pattern of descent with modification.

Darwin's Inspiration

How did Darwin arrive at his insight? To begin, Darwin had spent decades exploring and documenting the diversity of plants and animals, both around the globe and in his native England. So he had a wealth of data on variation within and among species, and he viewed this variation in the context of the ancient and changing Earth as popularized by his geologist friend, Charles Lyell.

All of this careful work gave Darwin an especially strong foundation in the pattern of evolution. To make sense of the process of evolution, Darwin turned in part to pigeon breeding—a model system that would be easier to study and manipulate than populations in the wild. Pigeon breeding was popular in England at the time, and in Darwin's words, "The diversity of the breeds is something astonishing" (see Figure 22.9).

Darwin crossbred pigeons and observed how characteristics were passed on to offspring. He could choose certain individuals with desirable traits to reproduce, thus manipulating the composition of the population by a process called **artificial selection.** It was clear to Darwin and other breeders that the diverse varieties were all descended from the wild rock pigeons.

Another influence on Darwin was the publication of a book by Thomas Robert Malthus, *An Essay on the Principle of Population*, which inspired heated discussion in England at the time.

Figure 22.9 Diversity of Pigeon Breeds in Captivity. Darwin used the breeding of pigeons as a model system to study how the characteristics of populations can change over time.

Malthus's studies of human populations in England and elsewhere led him to a startling conclusion: Since many more individuals are born than can survive, a "struggle for existence" occurs as people compete for food and places to live.

Darwin combined his observations of artificial selection with this notion of "struggle for existence" in natural populations, which he knew—from his countless studies—contained variation. From this synthesis arose his concept of natural selection. Although both Darwin and Wallace arrived at the same idea, Darwin's name is more closely associated with natural selection because of his extensive evidence for it in *On the Origin of Species*.

Darwin's Four Postulates

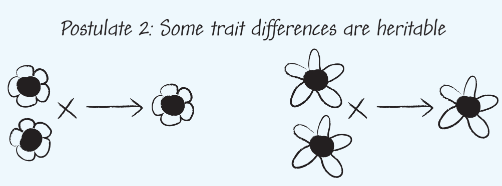
Darwin distilled the process of evolution by natural selection into four simple postulates (criteria) that form a logical sequence (see Making Models 22.2):

1. ***Variation exists among individual organisms that make up a population,*** such as variation in size and shape.
2. ***Some of the trait differences are heritable,*** meaning that they are passed on to offspring. For example, parent flowers with long petals tend to have offspring with long petals.
3. ***Survival and reproductive success is highly variable.*** Many more offspring are produced than can possibly survive. Thus, only some individuals in each generation survive long enough to produce offspring, and among the individuals that produce offspring, some will produce more than others.
4. ***The subset of individuals that survive best and produce the most offspring is not a random sample*** of the population. Instead, individuals with certain heritable traits are more likely to survive and reproduce.

Altogether, **natural selection** occurs when individuals with certain heritable traits produce more surviving offspring than do individuals without those traits. Thus, the frequency of the selected traits increases from one generation to the next. Biologists now know that traits are determined by alleles, particular versions of genes (see Chapter 14). Thus, the outcome of evolution by natural selection is a change in allele frequencies in a population over time (see Chapter 23).

Making Models 22.2 Tips on Drawing Darwin's Postulates

Drawing models can help you understand and remember abstract ideas such as Darwin's postulates. Simple drawings can be very effective, so focus on the ideas rather than trying to make lifelike illustrations. Consider this example:



MODEL Using the flower example shown here, make a model of Darwin's first postulate.

To see this model in action, go to https://goo.gl/cYtAHn

In studying these criteria, you should realize that variation among individuals in a population is essential if evolution is to occur. Darwin had to introduce population thinking into biology because it is populations that change over time. To come up with these postulates and understand their consequences, Darwin had to think in a revolutionary way.

Today, biologists usually condense Darwin's four postulates into a two-part statement that more forcefully communicates the essence of evolution by natural selection: Evolution by natural selection occurs when **(1)** heritable variation leads to **(2)** differential reproductive success.

The Biological Definitions of Fitness, Adaptation, and Selection

To explain the process of natural selection, Darwin referred to successful individuals as "more fit" than other individuals. In doing so, he gave the word "fitness" a definition different from its everyday English usage. Biological **fitness** is the ability of an individual to produce surviving, fertile offspring relative to that ability in other individuals in the population.

Note that fitness is a measurable quantity. When researchers study a population in the lab or in the field, they can estimate the relative fitness of individuals by comparing the number of surviving offspring each individual produces.

The concept of fitness, in turn, provides a compact way of formally defining adaptation. The biological meaning of adaptation, like the biological meaning of fitness, is different from its everyday English usage (see BioSkills 17). In evolutionary biology, an **adaptation** is a heritable trait that increases the fitness of an individual in a particular environment relative to individuals lacking the trait. Adaptations increase fitness—the ability to produce viable, fertile offspring. (You can see the Big Picture of how adaptation and fitness relate to natural selection on pages 516–517.)

Lastly, the term "selection" has a commonsense meaning in the context of artificial selection. Breeders *choose* which characteristics they want to keep or get rid of in their plant and animal breeds. However, selection has a very different meaning in the biological context of natural selection. Here, it refers to a passive process—differential reproduction as a result of heritable variation—not a purposeful choice.

22.4 Evolution in Action: Recent Research on Natural Selection

The theory of evolution by natural selection is testable, meaning biologists are able to test the validity of each of Darwin's postulates. Indeed, researchers have documented heritable variation and differential reproductive success in a wide array of natural populations.

This section summarizes two examples in which evolution by natural selection is observed in nature. Literally hundreds of other case studies are available, involving a wide variety of traits and organisms. To begin, let's explore the evolution of drug resistance, one of the great challenges facing today's biomedical researchers and physicians.

Case Study 1: How Did *Mycobacterium tuberculosis* Become Resistant to Antibiotics?

Mycobacterium tuberculosis, the bacterium that causes the infectious disease **tuberculosis**, or TB, has long been a scourge of humankind. It usually infects the lungs and causes fever, coughing, sweats, weight loss, and often death. In Europe and the United States, TB was once as great a public health issue as cancer is now. It receded in importance during the early 1900s, though, for two reasons:

1. Advances in nutrition made people better able to fight off most *M. tuberculosis* infections quickly.
2. The development of antibiotics allowed physicians to stop infections.

In the late 1980s, however, rates of *M. tuberculosis* infection surged in many countries, and in 1993 the World Health Organization declared TB a global health emergency. Physicians were particularly alarmed because the strains of *M. tuberculosis* responsible for the increase were largely or completely resistant to antibiotics that were once extremely effective.

How and why did the evolution of drug resistance occur? The case of a single patient—a young man who lived in Baltimore—illustrates what is happening all over the world.

A Patient History The story begins when the man was admitted to the hospital with fever and coughing. Chest X-rays, followed by bacterial cultures of fluid coughed up from the lungs, showed that he had an active TB infection. He was given several antibiotics for 6 weeks, followed by twice-weekly doses of the antibiotic rifampin for an additional 33 weeks. Ten months after therapy started, bacterial cultures from the patient's chest fluid indicated no *M. tuberculosis* cells. His chest X-rays were also normal. The antibiotics seemed to have cleared the infection.

Just two months after the TB tests proved normal, however, the young man was readmitted to the hospital with a fever, severe cough, and labored breathing. Despite being treated with a variety of antibiotics, including rifampin, he died of respiratory failure 10 days later. Samples of fluid from his lungs showed that *M. tuberculosis* was again growing actively there. But this time the bacterial cells were completely resistant to rifampin.

Drug-resistant *M. tuberculosis* cells had killed this patient. Where did they come from? Could a strain that was resistant to antibiotic treatment have evolved *within* him? To answer this question, a research team analyzed DNA from the drug-resistant strain and compared it with stored DNA from *M. tuberculosis* cells that had been isolated a year earlier from the same patient. After examining extensive stretches from each genome, the biologists were able to find only one difference: a point mutation in a gene called *rpoB*.

A Mutation in a Bacterial Gene Confers Resistance The *rpoB* gene codes for a component of RNA polymerase. This enzyme transcribes DNA to mRNA, so it is essential to the survival and reproduction of bacterial cells (see Chapter 17). In this case, the point mutation in the *rpoB* gene changed a cytosine to a thymine, forming a new allele for the *rpoB* gene (see Chapter 16). This missense mutation caused a change in the amino acid sequence of the RNA polymerase (from a serine to a leucine at the 153rd amino acid)—and a change in its shape.

This shape change proved critical. Rifampin, the antibiotic that was being used to treat the patient, works by binding to the RNA polymerase of *M. tuberculosis* and interfering with transcription. Bacterial cells with the C → T mutation continue to produce offspring efficiently even in the presence of the drug, because the drug cannot bind efficiently to the mutant RNA polymerase.

These results suggest the steps that led to this patient's death (**Figure 22.10**).

1. Completely by chance, one or a few of the bacterial cells present in the patient *before* the onset of drug therapy happened to have the *rpoB* allele with the C → T mutation. Under normal conditions, mutant forms of RNA polymerase do not work as well as the more common form, so cells with the C → T mutation would not produce many offspring and would stay at low frequency—even while the overall population grew to the point of inducing symptoms that sent the young man to the hospital.
2. Therapy with rifampin began. In response, cells in the population with normal RNA polymerase began to grow much more slowly or to die outright. As a result, the overall bacterial population declined in size so drastically that the patient appeared to be cured—his symptoms began to disappear.
3. Cells with the C → T mutation continued to increase in number after therapy ended. Eventually the *M. tuberculosis* population regained its former abundance, and the patient's symptoms reappeared.
4. Drug-resistant *M. tuberculosis* cells now dominated the population, so the second round of rifampin therapy failed.

✔ If you understand how antibiotic resistance evolves, you should be able to explain (1) why the relapse in step 3 occurred, and (2) whether a family member or health-care worker who got TB from this patient at step 3 or step 4 would respond to drug therapy.

Testing Darwin's Postulates Does the sequence of events illustrated in Figure 22.10 indicate that evolution by natural selection occurred? One way of answering this question is to review Darwin's four postulates and test whether each one was verified:

1. ***Did variation exist in the population?*** The answer is yes. Due to mutation, both resistant and nonresistant strains of TB were present before administration of the drug. Most *M. tuberculosis* populations, in fact, exhibit variation for the trait; studies on cultured *M. tuberculosis* show that a mutation conferring resistance to rifampin is present in one out of every 10^7 to 10^8 cells.
2. ***Was this variation heritable?*** The answer is yes. The researchers showed that the variation in the phenotypes of the two strains—from drug susceptibility to drug resistance—was due to variation in their genotypes. Because the mutant *rpoB* gene is passed on to daughter cells when a *Mycobacterium* replicates, the allele and the phenotype it produces—drug resistance—are passed on to offspring.
3. ***Was there variation in survival and reproductive success?*** The answer is yes. Only a tiny fraction of *M. tuberculosis* cells in the patient survived the first round of antibiotics long enough to reproduce. Most cells died and left no or almost no offspring.
4. ***Were survival and reproduction nonrandom?*** The answer is yes. When rifampin was present, certain cells—those with the drug-resistant allele—had higher reproductive success than cells with the normal allele.

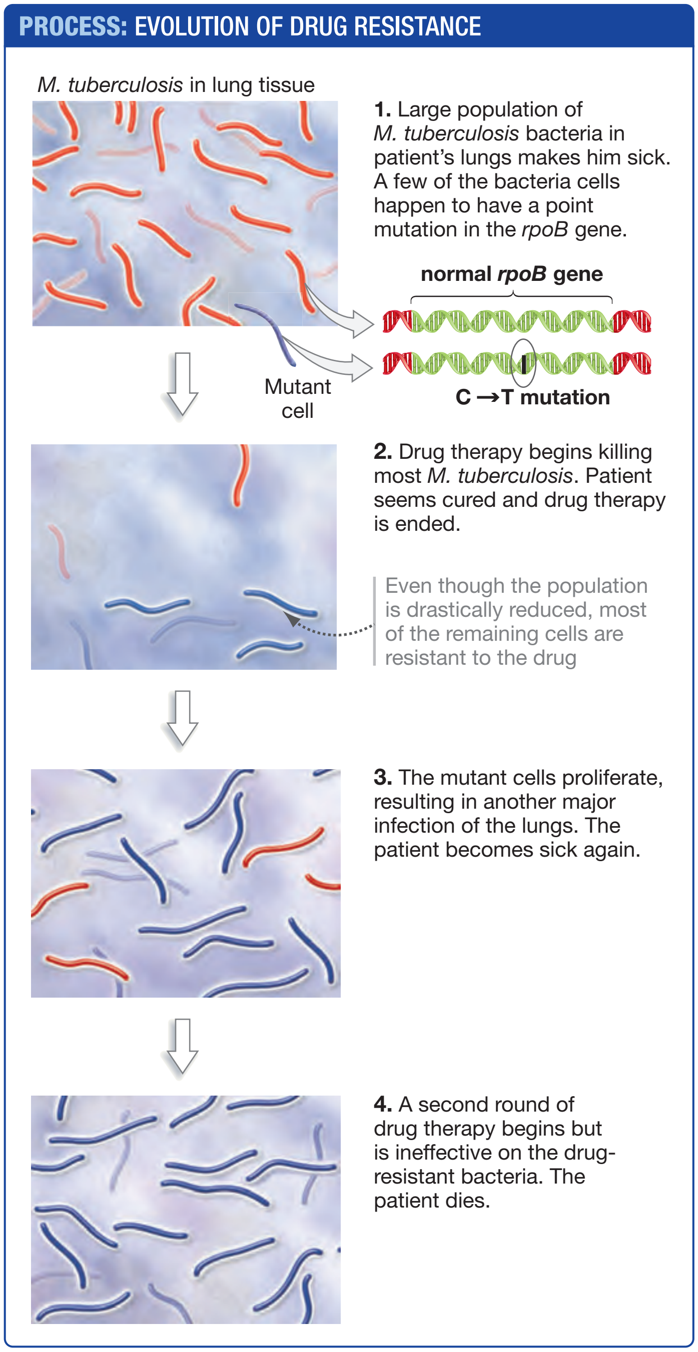


Figure 22.10 Alleles That Confer Drug Resistance Increase in Frequency when Drugs Are Used.

M. tuberculosis individuals with the mutant *rpoB* allele had higher fitness in an environment where rifampin was present. The mutant allele produces a protein that is an adaptation when the cell's environment contains the antibiotic.

This study verified all four postulates and confirmed that evolution by natural selection had occurred. The *M. tuberculosis* population evolved because the mutant *rpoB* allele increased in frequency.

It is critical to note, however, that the individual cells themselves did not evolve—they could not mutate their genes in order to survive the antibiotics. When natural selection occurred, the individual bacterial cells simply survived or died, or produced more or fewer offspring. This is a fundamentally important point: Natural selection acts on individuals, because individuals experience differential reproductive success. But only populations evolve. Allele frequencies change in populations, not in individuals. Understanding evolution by natural selection requires population thinking.

Drug Resistance: A Widespread Problem The events reviewed for this single patient have occurred many times in other patients. Recent surveys indicate that drug-resistant strains now account for about 10 percent of the *M. tuberculosis*–causing infections throughout the world.

Unfortunately, the emergence of drug resistance in TB is far from unusual. Resistance to a wide variety of antibiotics is skyrocketing globally due to the escalating use of antibiotics in applications ranging from toothpaste to livestock feed. Consider the prevalence in hospitals of the bacterium *Staphylococcus aureus* that are resistant to the antibiotic vancomycin (**Figure 22.11**). Most of these *S. aureus* cells are also resistant to methicillin and other antibiotics—a phenomenon known as multidrug resistance. In some cases, physicians have no effective antibiotics available to treat these infections. The incidence of antibiotic resistance has risen so quickly that the World Health Organization recently announced that the world could soon enter a "post-antibiotic era."

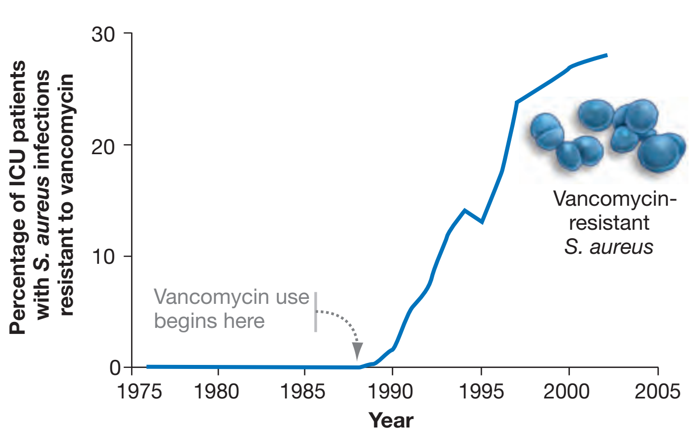


Figure 22.11 Trends in Infections Due to Antibiotic-Resistant Bacteria. The line indicates changes in the percentage of infections caused by the bacterium *Staphylococcus aureus,* acquired in the intensive care unit (ICU) of hospitals in the United States, that are resistant to the antibiotic vancomycin.

DATA: Centers for Disease Control, 2004.

Further, resistance to a wide variety of insecticides, fungicides, antiviral drugs, and herbicides has evolved in hundreds of insects, fungi, bacteria, viruses, and plants. In every case, evolution has occurred because the original population included individuals with the heritable ability to resist some chemical compound. As the susceptible individuals died from the pesticide, herbicide, or drug, the alleles that confer resistance increased in frequency.

Case Study 2: Why Do Beak Sizes and Shapes Vary in Galápagos Finches?

Human use of antibiotics has clearly influenced the evolution of some bacterial species. Have biologists also observed evolution caused by natural environmental changes? The answer is certainly yes. As an example, consider research led by Peter and Rosemary Grant. For over four decades, these biologists have been investigating changes in beak size, beak shape, and body size that have occurred in finches native to the Galápagos Islands.

Because the island of Daphne Major of the Galápagos is so small—about the size of 80 football fields (see tiny dot between Santiago and Santa Cruz in Figure 22.6)—the Grants' team has been able to catch, weigh, and measure all the medium ground finches in the island's population (**Figure 22.12**) and mark each one with a unique combination of colored leg bands. The medium ground finch makes its living by eating seeds. Finches crack seeds with their beaks.

Early studies of the finch population established that beak size and shape and body size vary among individuals, and that beak morphology and body size are heritable. More specifically, parents with particularly deep beaks tend to have offspring with deep beaks. Large parents also tend to have large offspring. Beak size and shape and body size are traits with heritable variation.

Selection during Drought Conditions Not long after the team began to study the finch population, a dramatic selection event occurred. In the annual wet season of 1977, Daphne Major received just 24 millimeters (mm) of rain instead of the 130 mm that normally falls. During the drought, few plants were able to produce seeds, and 84 percent (about 660 individuals) of the medium ground finch population disappeared.

Two observations support the hypothesis that most or all of these individuals died of starvation:

1. The researchers found 38 dead birds, and all were emaciated.
2. None of the missing individuals were spotted on nearby islands, and none reappeared once the drought had ended and food supplies returned to normal.

The research team realized that the die-off was a **natural experiment.** Instead of comparing groups created by direct manipulation under controlled conditions, natural experiments allow researchers to compare treatment groups created by an unplanned change in conditions. In this case, the Grants' team could test whether natural selection occurred by comparing the population before and after the drought.

Figure 22.12 The Grants' Field Site in the Galápagos.

Were the survivors different from nonsurvivors? The histograms in **Figure 22.13** show the distribution of beak sizes in the population before and after the drought. Notice the different scales of the *y*-axes of the two graphs. (For more on how histograms are constructed, see **BioSkills 2**.) On average, survivors tended to have much deeper beaks than did the birds that died.

Why were deeper beaks adaptive? At the peak of the drought, most seed sources were absent and the tough fruits of a plant called *Tribulus cistoides* served as the finches' primary food source. These fruits are so difficult to crack that finches ignore them in years when food supplies are normal. The Grants hypothesized that individuals with particularly large and deep beaks were more likely to crack these fruits efficiently enough to survive.

At this point, the Grants had shown that natural selection led to an increase in average beak depth in the population. When breeding resumed in 1978, the offspring produced had beaks that were half a millimeter deeper, on average, than those in the population that existed before the drought. This result confirmed that evolution had occurred. In only one generation, natural selection led to a measurable change in the heritable characteristics of the population. Large, deep beaks were an adaptation for cracking large fruits and seeds.

Continued Changes in the Environment, Continued Selection, Continued Evolution In 1983, the environment on the Galápagos Islands changed again. Over a seven-month period, a total of 1359 mm of rain fell. Plant growth was luxuriant, and finches fed primarily on the small, soft seeds that were being produced in abundance. During this interval, individuals with small, shallow beaks had exceptionally high reproductive success—meaning that they had higher fitness than those with large, deep beaks—because they were better able to harvest the small seeds. As a result, the characteristics of the population changed again.

RESEARCH

QUESTION: Did natural selection on ground finches occur when the environment changed?

HYPOTHESIS: Beak characteristics changed in response to a drought.

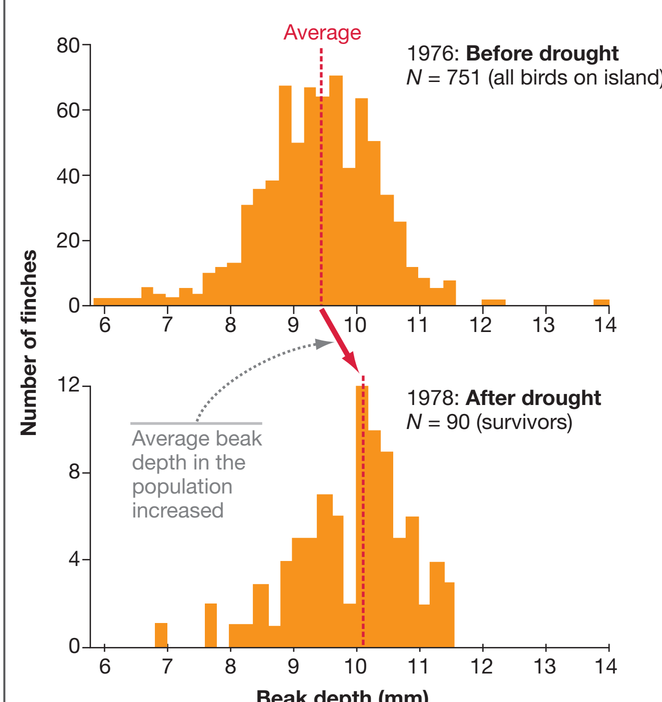
NULL HYPOTHESIS: No changes in beak characteristics occurred in response to a drought.

EXPERIMENTAL SETUP:

PREDICTION:

PREDICTION OF NULL HYPOTHESIS:

RESULTS:



CONCLUSION: Natural selection occurred. The characteristics of the population have changed.

Figure 22.13 A Natural Experiment: Changes in a Medium Ground Finch Population in Response to a Change in the Environment (a Drought). The results show the distribution of beak depth in the population of medium ground finches on Daphne Major before and after the drought of 1977. *N* is the population size.

SOURCE: Boag, P. T., and P. R. Grant. 1981. Intense natural selection in a population of Darwin's finches (Geospizinae) in the Galápagos. *Science* 214: 82–85.

✔ **PROCESS OF SCIENCE** Fill in both predictions.

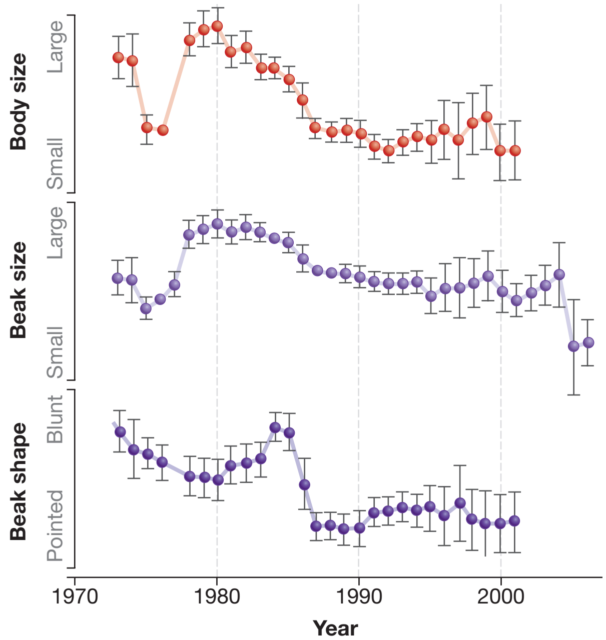


Figure 22.14 Body Size, Beak Size, and Beak Shape in Finches Fluctuated over a 35-Year Interval. Each of the dependent variables is a mathematical composite of three measurements. Body size is calculated from body mass, wing length, and leg length. Beak size and shape are calculated from beak depth, length, and width.
DATA: Grant, P. R., and B. R. Grant. 2002. *Science* 296: 707–711; Grant, P. R., and B. R. Grant. 2006. *Science* 313: 224–226.

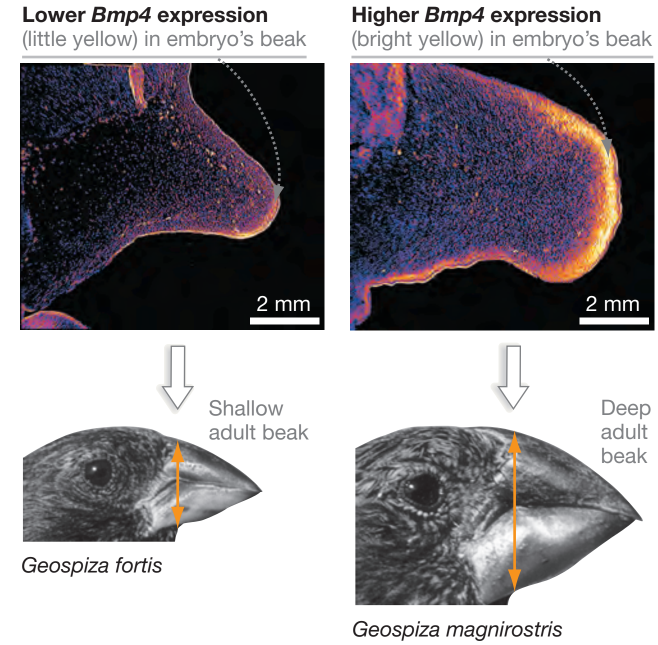


Figure 22.15 Changes in *Bmp4* Expression Change Beak Depth. These micrographs are in situ hybridizations showing the location and extent of *Bmp4* expression in young *Geospiza fortis* and *G. magnirostris*. In these and four other species that were investigated, the amount of Bmp4 protein produced correlates with the depth of the adult beak.

Beak size and depth are only two of the many characteristics that the Grants documented over time. **Figure 22.14** shows changes that have occurred in three characteristics—average body size, beak size, and beak shape—over 35 years. Long-term studies like this are powerful because they have succeeded in documenting natural selection in response to changes in the environment. The take-home message from the data is that most traits are not inherently "good" or "bad"—the adaptive value of a trait depends on context, and context can change over time. ✔ **CAUTION Evaluate this statement in the context of the finch data: "Bigger is always better." How do the error bars (see BioSkills 3) affect your evaluation?**

Which Genes Are under Selection? Characteristics like body size and beak shape are polygenic, meaning that many genes—each one exerting a relatively small effect—influence the trait (see Chapter 14). Because many genes are involved, it can be difficult for researchers to know exactly which alleles are changing in frequency when polygenic traits evolve.

To explore which of the medium ground finch's genes might be under selection, researchers in Clifford Tabin's lab began studying beak development in an array of Galápagos finch species. Specifically, they looked for variation in the pattern of expression of cell–cell signals that had already been identified as important in the development of chicken beaks. The hope was that homologous genes might affect beak development in finches. The researchers struck gold when they carried out in situ hybridization (a technique featured in Chapter 21) showing where a cell–cell signal gene called *Bmp4* is expressed.

- As in chickens, there is a strong correlation between the amount of *Bmp4* expression when beaks are developing in young Galápagos finches and the depth of adult beaks (**Figure 22.15**).
- Further, when the researchers experimentally increased *Bmp4* expression in young chickens, they found that beaks got deeper than normal. This is evidence of a causal relationship between *Bmp4* expression and beak depth, not just a correlation.

The Grants have recently collaborated with a team of geneticists to sequence the genomes of 120 birds representing all of the finch species on the Galápagos. Among other insights, this research has pinpointed another gene that appears to play an important role in the regulation of beak shape, *ALX1*. The frequencies of different alleles of *ALX1* are highly correlated with beak shape. This same gene is important in the development of human facial structures.

CHECK YOUR UNDERSTANDING

If you understand that . . .

- If individuals with certain alleles produce the most offspring in a population, then those alleles increase in frequency over time. Evolution results from this process of natural selection on heritable variation.

✔ You should be able to . . .

1. Apply Darwin's four postulates to the Galápagos finch case study to verify that natural selection has occurred.
2. **MODEL** Use simple sketches of finches with different beak depths to illustrate how Darwin's four postulates apply in the finch case study.

Answers are available in Appendix A.

22.5 Debunking Common Myths about Natural Selection and Adaptation

Evolution by natural selection is a simple process—just the logical outcome of some straightforward postulates. However, natural selection and population thinking are relatively new concepts in the scope of human culture. After more than two thousand years of belief in typological thinking, the scale of nature, and goal-oriented evolution (Section 22.1), a great deal of cultural inertia has fostered myths about evolution by natural selection (see BioSkills 17). Let's consider three of the most common types of misconceptions about natural selection, summarized in Table 22.3.

Natural Selection Does Not Change Individuals

Perhaps the most important point to clarify about natural selection is that during the process, individuals do not change—only the population does. During the drought, the beaks of individual finches did not become deeper. Rather, the average beak depth in the population increased over time because deep-beaked individuals survived and produced more offspring than shallow-beaked individuals did. Natural selection acted on individuals, but the evolutionary change occurred in the characteristics of the population.

In the same way, individual *M. tuberculosis* cells did not change when rifampin was introduced to their environment. Each of these bacterial cells had the same RNA polymerase allele throughout its life. But because the mutant allele increased in frequency in the population over time, the average characteristics of the bacterial population changed.

Natural Selection Is Not "Lamarckian" Inheritance There is a sharp contrast between evolution by natural selection and evolution by the inheritance of acquired characters—the hypothesis promoted by Jean-Baptiste de Lamarck. If you recall, Lamarck proposed that **(1)** individuals change in response to challenges posed by the environment (such as giraffes stretching their necks to reach leaves high in the treetops), and **(2)** the changed traits are then passed on to offspring. The key claim is that the important evolutionary changes occur in individuals.

In contrast, Darwin realized that individuals do not change when they are selected. Instead, they simply produce more or fewer offspring than other individuals do. When this happens, alleles found in the selected individuals become more or less frequent in the population.

Darwin was correct: There is no mechanism that makes it possible for natural selection to edit the nucleotide sequence of an allele inside an individual. An individual's heritable characteristics don't change when natural selection occurs. Natural selection sorts existing variants—it doesn't change them.

Acclimatization Is Not Adaptation The issue of change in individuals is tricky because individuals often *do* change in response to changes in the environment. For example, if you were to travel to the Tibetan Plateau in Asia, your body would experience oxygen deprivation due to the low partial pressure of oxygen at high elevations (see Chapter 42). As a result, your body would produce more of the oxygen-carrying pigment hemoglobin and more hemoglobin-carrying red blood cells. Your body does not normally produce more red blood cells than it needs, because viscous (thick) blood can cause a disease—chronic mountain sickness—that can lead to heart failure.

The increase in red blood cells is an example of what biologists call **acclimatization**—a change in an individual's phenotype that occurs in response to a change in natural environmental conditions. (When this process occurs in study organisms in a laboratory, it is called **acclimation**.) Phenotypic changes due to acclimatization

SUMMARY Table 22.3
Common Misconceptions, Corrected

Misconception	Example
"Evolutionary change occurs in organisms" CORRECTION: • Natural selection just sorts existing variants in organisms; it doesn't change them • Evolutionary change occurs only in populations • Acclimatization ≠ adaptation Selection does not cause neck length to increase in individual giraffes, only in populations	
"Evolution is goal directed" CORRECTION: • Adaptations do not occur because organisms want or need them • Mutation, the source of new alleles, occurs by chance • Evolution is not progressive • Loss of traits can be adaptive • There is no such thing as a higher or lower organism Roses cannot grow thorns on purpose to deter herbivores	
"Evolution perfects organisms" CORRECTION: • Not all traits are adaptive • Some traits cannot be optimized due to fitness trade-offs • Some traits are limited by genetic, historical, or environmental constraints Humans lack the ability to grow wings, even though flight could be an adaptive trait	

Figure 22.16 Adaptation has a different meaning in science than in everyday life. In 1953, New Zealand mountaineer Edmund Hillary (left) and Tibetan sherpa Tenzing Norgay (right) were the first humans to reach the highest mountain peak in the world, the summit of Mount Everest. Climbers must *acclimatize* slowly to extremely high altitudes to avoid "mountain sickness," but sherpas like Norgay also have *adaptations* to life at high altitudes—genetically determined characteristics that improve their ability to survive in the mountains.

are not passed on to offspring, because no alleles have changed. As a result, acclimatization does not cause evolution.

In contrast, populations that have lived in Tibet for many generations are adapted to this environment through genetic changes. Among native Tibetans, for example, an allele that increases the ability of hemoglobin to hold oxygen has increased to high frequency. In populations that do not live at high elevations, this allele is rare or nonexistent (see Figure 22.16). ✔ **CAUTION If you understand adaptation, you should be able to explain the difference between the evolutionary definition of adaptation and its use in everyday English.**

Natural Selection Is Not Goal Directed

It is tempting to think that evolution by natural selection is goal directed. But adaptations do not occur because organisms want or need them.

Mutations Occur by Chance Mutations are the source of new alleles, but mutations occur by chance and are random with respect to fitness—they do not occur to solve problems. For example, you might hear a fellow student say that Tibetans "needed" the new hemoglobin allele so that they could survive at high altitudes, or that *M. tuberculosis* cells "wanted" the drug-resistant allele so that they could survive and continue to reproduce in an environment that included rifampin. This purposeful change does not happen.

The mutations that created the mutant alleles in both examples occurred randomly, due to errors in DNA synthesis, and they just happened to be advantageous when the environments changed. There is no mechanism that enables the environment to direct which mistakes DNA polymerase makes when copying genes. Mutations just happen. ✔ **CAUTION If you understand how mutations occur, you should be able to explain how thorns originated in roses.**

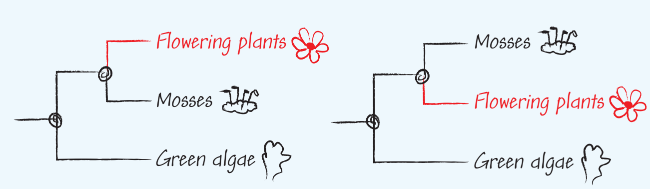
Evolution Is Not Progressive It is often appealing to think that evolution by natural selection is progressive—meaning organisms have gotten better over time. (In this context, "better" usually means bigger, stronger, or more complex.) And it is true that groups appearing later in the fossil record are often more morphologically complex than closely related groups that appeared earlier: For example, flowering plants are considered more complex than mosses. But there is nothing predetermined or absolute about this tendency.

In fact, complex traits are routinely lost or simplified over time as a result of evolution by natural selection. You've already analyzed evidence documenting limb loss in whales (Section 22.2). Populations that become parasitic are particularly prone to loss of complex traits. For example, the tapeworm parasites of humans and other mammals have lost their sophisticated digestive tracts and mouths due to natural selection—tapeworms are well adapted to absorb nutrients directly from their environment.

There Is No Such Thing as a Higher or Lower Organism The nonprogressive nature of evolution by natural selection contrasts sharply with Lamarck's conception of the evolutionary process, in which organisms progress over time to higher and higher levels on a scale of nature (see Figure 22.1c). Under Aristotle's and Lamarck's hypotheses, it is sensible to refer to "higher" and "lower" organisms. But under evolution by natural selection, there is no such thing as a higher or lower organism (see Figure 22.1d). For example, mosses may be a more ancient group than flowering plants, but neither group is higher or lower than the other (see Making Models 22.3). Mosses simply have a different suite of adaptations than do flowering plants, so they thrive in different types of environments.

Making Models 22.3 Tips on Drawing Phylogenetic Trees

Phylogenetic trees can be challenging to interpret and draw (see **BioSkills 13** and Chapter 25). Note that the labels on the branch tips are not arranged in a "lower to higher" order. Rather, branches can be rotated around the nodes (marked by dots) without changing their relationships.



These trees have the same meaning

MODEL Draw a third tree with the same meaning as the two shown here by rotating the green algae branch to the top.

To see this model in action, go to https://goo.gl/nTB7hh

Natural Selection Does Not Lead to Perfection

Although organisms are often exquisitely adapted to their environment, adaptation is far from perfect. A long list of circumstances limits the effectiveness of natural selection; only a few of the most important ones are discussed here.

Traits Are Not Always Adaptive Vestigial traits such as the human coccyx (tailbone) and the tiny hindlimbs of early whales do not increase the fitness of individuals with those traits. The structures are not adaptive. They exist because they were present in the ancestral population.

Vestigial traits are not the only types of structures with no or reduced function. Perhaps the best example of nonadaptive traits involves evolutionary changes in DNA sequences. A mutation may change a base in the third position of a codon without changing the amino acid sequence of the protein encoded by that gene. Changes such as these are said to be silent. They occur due to the redundancy of the genetic code (see Chapter 16). Silent changes in DNA sequences are extremely common. But because they don't change the phenotype, they can't be acted on by natural selection and are not adaptive.

Fitness Trade-offs Exist In everyday English, the term "trade-off" refers to a compromise between competing goals. It is difficult to design a car that is both large and fuel efficient, a bicycle that is both rugged and light, or a plane that is both steady and maneuverable.

In nature, selection occurs in the context of fitness trade-offs. A **fitness trade-off** (or simply **trade-off**) is a compromise between two traits that cannot be optimized simultaneously. In medium ground finches, for example, there is a trade-off between having a beak that is large and deep enough to crack open tough seeds and one that is small and shallow enough to extract tiny seeds. Similarly, there is a trade-off between bright coloration to attract mates and cryptic coloration to hide from predators.

Many types of trade-offs occur due to energetic constraints, because every individual has a restricted amount of time and energy available—meaning that its resources are limited. For example, there is a trade-off between the size of eggs or seeds that an individual makes and the number of offspring it can produce (Chapter 51) and a trade-off between investing energy in reproduction versus immune function (Chapter 39). The message of these findings is simple: Because selection acts on many traits at once, every adaptation is a compromise.

Traits Are Genetically Constrained The studies on *Bmp4* expression in developing finch beaks (see Figure 22.15) produced an interesting observation—increased *Bmp4* expression resulted in beaks that were not only deeper but also wider in their side-to-side dimension. This common pattern is due to **genetic correlation**. Genetic correlations occur because of pleiotropy, in which a single gene affects multiple traits (see Chapter 14). In this case, selection on a gene for one trait (increased beak depth) caused a correlated, though not necessarily adaptive, increase in another trait (beak width). As it turns out, a finch beak that is deep but narrow from side to side would be more effective at twisting open tough *Tribulus* fruits, but this phenotype was never produced due to genetic constraints.

Genetic correlations are not the only genetic constraint on adaptation. Lack of genetic variation is also important. Consider that salamanders have the ability to regrow severed limbs. Some eels and sharks can sense electric fields. Birds can see ultraviolet light. Even though these traits would possibly confer increased reproductive success in humans, they do not exist—because humans lack the necessary genes.

Traits Are Historically Constrained In addition to being constrained by fitness trade-offs, genetic correlations, and lack of genetic variation, adaptations are constrained by history. The reason is simple: All traits evolve from previous traits.

Natural selection can change the function of structures dramatically over time. For example, the tiny incus, malleus, and stapes bones found in your middle ear evolved from bones that were either part of the jaw or supported the jaw in the ancestors of mammals. These bones now function in transmitting and amplifying sound from your outer ear to your inner ear. Biologists routinely interpret these bones as adaptations that improve your ability to hear airborne sounds. But are the bones a "perfect" solution to the problem of transmitting sound from the outside of the ear to the inside? The answer is no. They are a good solution, given an important historical constraint. Other vertebrates have different structures involved in transmitting sound to the ear. In at least some cases, those structures may be more efficient than our incus, malleus, and stapes.

Traits Are Environmentally Constrained Natural selection often occurs in the context of a changing environment. Recall that the amount of rain fluctuates on Daphne Major in the Galápagos Islands, causing dramatic changes in vegetation and seed availability over time. Thus, a beak shape that is adaptive in one season may not be adaptive in the next season, preventing the "perfection" of beak shape in the finch population (see Figure 22.14).

In addition to fluctuating over time, the abiotic and biotic features of the environment can change over the geographic range of the population. For example, one of the most notorious invasive plants in North America, purple loosestrife, has spread from the southern United States into Canada over a distance of 1000 km in less than a century. In the south, where the growing season is long, it is adaptive for purple loosestrife to grow large and then flower late. But in the north, it is more adaptive for purple loosestrife to grow less and flower early. No growth rate or flowering time is optimal for all environments.

Some environmental events are so catastrophic that organisms are wiped out regardless of which adaptations they have. These chance events, such as volcanic eruptions, asteroid impacts, and deforestation by humans, can cause a change in the average traits of a population that are random with respect to fitness.

To summarize, not all traits are adaptive, and even adaptive traits are constrained by genetic, historical, and environmental factors. In addition, natural selection is not the only process that causes evolutionary change. Three other processes—genetic drift, gene flow, and mutation—change allele frequencies over time (see Chapter 23). Compared with natural selection, these processes have very different consequences. (You can see the Big Picture of how natural selection relates to other evolutionary processes on pages 516–517.)

22.1 The Rise of Evolutionary Thought

- Plato, Aristotle, and several religious texts present species as unchanging types. This view is called typological thinking.
- Lamarck proposed a theory of evolution—that species are not static but change through time. He proposed that evolution occurs by the inheritance of acquired characteristics.
- Darwin and Wallace proposed that evolution occurs by natural selection. This was the beginning of population thinking, whereby variation among individuals is the key to understanding evolution.

22.2 The Pattern of Evolution: Have Species Changed, and Are They Related?

- Evidence that species change through time includes data on **(1)** Earth's age and the fact of extinction; **(2)** the resemblance of modern to fossil forms in the same area; **(3)** transitional features in fossils; **(4)** the presence of vestigial traits; and **(5)** change in contemporary populations.
- The consensus that species are related by common ancestry is supported by data on **(1)** the geographic proximity of closely related species; **(2)** the existence of genetic, developmental, and structural homologies; and **(3)** the contemporary formation of new species from preexisting species.
- Evidence for evolution is internally consistent, meaning that data from several independent sources are mutually reinforcing.

22.3 The Process of Evolution: How Does Natural Selection Work?

- Darwin developed four postulates that outline the process of evolution by natural selection. These postulates can be summarized by the following statement: Heritable variation leads to differential reproductive success.
- Alleles or traits that increase the reproductive success of an individual are said to increase the individual's fitness. A trait that leads to higher fitness, relative to individuals without the trait, is an adaptation. If a particular allele increases fitness and leads to adaptation, the allele will increase in frequency in the population.

22.4 Evolution in Action: Recent Research on Natural Selection

- Selection by drugs on the TB bacterium and changes in the size and shape of finch beaks in the Galápagos as a result of seed availability are well-studied examples of natural selection.
- Both examples demonstrate that evolution can be observed and measured. Evolution by natural selection has been confirmed by a wide variety of studies and is considered to be a central organizing principle of biology.

22.5 Debunking Common Myths about Natural Selection and Adaptation

- Natural selection acts on individuals, but evolutionary change occurs in populations. Nonheritable changes that occur in individuals due to acclimatization or acclimation are not adaptations and do not result in evolution.
- Evolution is not goal directed and does not lead to perfection. Mutations occur by chance, not because organisms "want" or "need" them to survive. There is no such thing as a higher or lower organism.
- Not all traits are adaptive, and even adaptive traits are limited by fitness trade-offs and genetic, historical, and environmental constraints.

Answers are available in Appendix A

✔ TEST YOUR KNOWLEDGE

1. True or false? Some traits are considered vestigial because they existed long ago.

2. **CAUTION** Why does the presence of extinct forms and transitional features in the fossil record support the pattern component of the theory of evolution by natural selection?
   - **a.** It supports the hypothesis that individuals change over time.
   - **b.** It supports the hypothesis that weaker species are eliminated by natural selection.
   - **c.** It supports the hypothesis that species evolve to become more complex and better adapted over time.
   - **d.** It supports the hypothesis that species change over time.

3. Traits that are derived from a common ancestor, like the bones of human arms and bird wings, are said to be ________.

4. **CAUTION** How can evolutionary fitness be estimated?
   - **a.** Document how long individuals survive.
   - **b.** Count the number of healthy, fertile offspring produced.
   - **c.** Determine which individuals are strongest.
   - **d.** Determine which phenotype is the most common.

✔ TEST YOUR UNDERSTANDING

5. **CAUTION** According to data presented in this chapter, which one of the following statements is correct?
   - **a.** When individuals change in response to challenges from the environment, their altered traits are passed on to offspring.
   - **b.** Species are created independently of each other and do not change over time.
   - **c.** Populations—not individuals—change when natural selection occurs.
   - **d.** The traits of populations become more perfect over time.

6. Some biologists summarize evolution by natural selection with the phrase "mutation proposes, selection disposes." Mutation is a process that creates heritable variation. Explain what the phrase means.

7. **CAUTION** Why don't the biggest and strongest individuals in a population always produce the most offspring?
   a. The biggest and strongest individuals always have higher fitness.
   b. In some environments, being big and strong lowers fitness.
   c. Sometimes the biggest and strongest individuals may choose to have fewer offspring.
   d. Sometimes the number of offspring is not related to fitness.
8. **SOCIETY** Explain why the overprescription of antibiotics by doctors, or the overuse of everyday soaps containing antibiotics, can be a health risk.

✔ TEST YOUR PROBLEM-SOLVING SKILLS

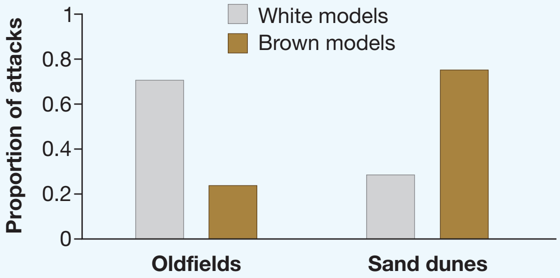
9. The average height of humans in industrialized nations has increased steadily for the past 100 years. This trait has clearly changed over time. Most physicians and human geneticists hypothesize that the change is due to better nutrition and a reduced incidence of disease. Has human height evolved?
   a. Yes, because average height has changed over time.
   b. No, because changes in height due to nutrition and reduced incidence of disease are not heritable.
   c. Yes, because height is a heritable trait.
   d. No, because height is not a heritable trait.
10. **PROCESS OF SCIENCE** The geneticist James Crow wrote that successful scientific theories have the following characteristics: (1) They explain otherwise puzzling observations; (2) they provide connections between otherwise disparate observations; (3) they make predictions that can be tested; and (4) they are heuristic, meaning that they open up new avenues of theory and experimentation. Crow added two other elements of scientific theories that he considered important on a personal, emotional level: (5) They should be elegant, in the sense of being simple and powerful; and (6) they should have an element of surprise. How well does the theory of evolution by natural selection fulfill these six criteria?

✔ PUT IT ALL TOGETHER: Case Study

How can natural selection on mouse color be measured?

Most mice living on the mainland of Florida are brown, but the mice that live on the sand dunes of the barrier islands have white fur (see Chapter 16). It is intuitive that the light color of beach-dwelling mice is an adaptation for blending into their environment—and thus evading predators. How can this hypothesis be tested?

11. Compare and contrast how evolution by inheritance of acquired characters and the theory of evolution by natural selection would explain the observation of white mice living on light soil and brown mice living on dark soil.
12. **CAUTION** What is an evolutionary adaptation?
    a. a trait that improves the fitness of its bearer, compared with individuals without the trait
    b. a trait that changes in response to environmental influences within the individual's lifetime
    c. the ability of an individual to adjust to its environment
    d. a trait that an individual wants so that it can survive
13. Apply Darwin's four postulates to a population of mice living on sand dunes in coastal Florida.
14. **PROCESS OF SCIENCE** A team lead by evolutionary biologist Hopi Hoekstra set out to test the hypothesis that predators are an agent of natural selection on mouse color. They made 250 plasticine models of mice that were alike in every way except that half were painted white and half were painted brown. Suggest one advantage and one disadvantage of using model mice instead of real mice in this experiment.
15. **QUANTITATIVE** The researchers placed white and brown mouse models both in abandoned fields, called oldfields, on the mainland (dark soil) and on sand dunes on the islands (light soil) and then measured the percentage of models that were attacked by predators. What is the take-home message of the data? Do the data support or reject the hypothesis that mouse color is adaptive?



Source: Vignieri, S. N., J. G. Larson, and H. E. Hoekstra. 2010. *Evolution* 64: 2153–2158.

16. **PROCESS OF SCIENCE** When a statistical test was used to compare the results for white models versus brown models, the P value (see BioSkills 3) was 0.01 for each habitat. Does this result increase or decrease your confidence in your take-home message? Explain.