a. Large, ground-dwelling finch

b. Warbler finch

c. Cactus-finch

FIGURE 15.10 Galápagos finches.

Each of the present-day 13 species of finches has a beak adapted to a particular way of life. For example, (**a**) the heavy beak of the large ground-dwelling finch (*Geospiza magnirostris*) is suited to a diet of large seeds; (**b**) the beak of the warbler-finch (*Certhidea olivacea*)is suited to feeding on insects found among ground vegetation or caught in the air; and (**c**) the longer beak, somewhat decurved, and the split tongue of the cactus-finch (*Cactornis scandens*) are suited to probing a cactus for seeds.

Natural Selection Can Be Witnessed

Darwin had formed his natural selection hypothesis by observing the distribution of tortoises and finches on the Galápagos Islands. Tortoises with domed shells and short necks live on well-watered islands, where grass is available. Those with shells that flare up in front have long necks and are able to feed on cacti. They live on arid islands, where treelike prickly-pear cactus is the main food source. Similarly, the islands are home to many different types of finches. The heavy beak of the large, ground-dwelling finch is suited to a diet of seeds. The thin, sharp beak of a warbler-finch is able to probe vegetation for and spear insects, while the decurved beak of a cactus-finch can find and feed on cactus seeds (Fig. 15.10).

Today, investigators, such as Peter and Rosemary Grant of Princeton University, are actually watching natural selection as it occurs. In 1973, the Grants began a study of the various finches on Daphne Major, near the center of the Galápagos Islands. The weather swung widely back and forth from wet years to dry years, and they found that the beak size of the medium ground finch, *Geospiza fortis*, adapted to each weather swing, generation after generation (Fig. 15.11). These finches like to eat small, tender seeds that require a smaller beak, but when the weather turns dry, they have to eat larger, drier seeds, which are harder to crush. The birds that have a larger beak depth have an advantage and have more offspring. Therefore, among the next generation of *G. fortis* birds, the beak size has more depth than the previous generation.

Among other examples, the shell of the marine snail *(Littorina obtusata*) has changed over time, probably due to being heavily hunted by crabs. Also, the beak length of the scarlet honeycreeper (*Vestiaria coccinea)* was reduced when the bird switched to a new source of nectar because its favorite flowering plants, the lobelloids, were disappearing.

A much-used example of natural selection is industrial melanism. Prior to the Industrial Revolution in Great Britain, light-colored peppered moths, *Biston betularia*, were more common than dark-colored peppered moths. It was estimated that only 10% of the moth population was dark at this time. With the advent of industry and an increase in pollution, the number of dark-colored moths exceeded 80% of the moth population. After legislation to reduce pollution, a dramatic reversal in the ratio of light-colored moths to dark-colored moths occurred. In 1994, one collecting site recorded a drop in the frequency of dark-colored moths to 19%, from a high of 94% in 1960.

The rise in bacterial resistance to antibiotics has occurred within the past 30 years or so. Resistance is an expected way of life now, not only in medicine, but also in agriculture. New chemotherapeutic and HIV drugs are required because of the resistance of cancer cells and HIV, respectively. Also, pesticides and herbicides have created resistant insects and weeds.

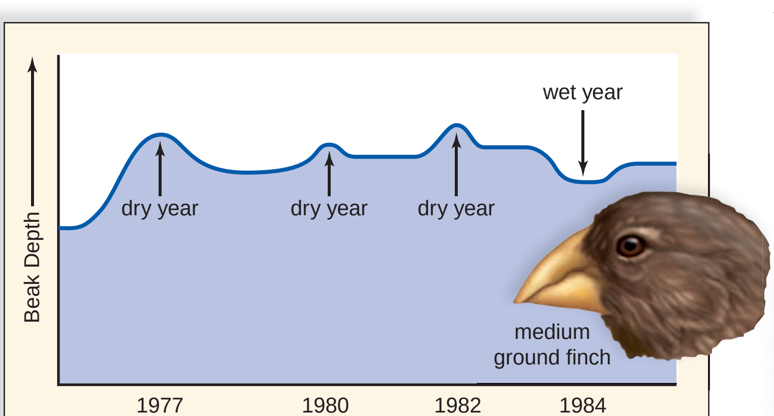


FIGURE 15.11 Beak depth.

The beak depth of a ground finch varies from generation to generation, according to the weather.

Check Your Progress 15.2

1. What characteristic must a population first have for the process of natural selection to occur?
2. Hypothetically, the members of a rabbit population vary as to length of fur. Some members of the population migrate up a mountain, where it is much colder. After many generations, what would the fur length of rabbits likely be at the bottom and top of the mountain? Explain.

15.3 Evidence for Evolution

Many different lines of evidence support the hypothesis that organisms are related through common descent. This is significant, because the more varied the evidence supporting a hypothesis, the more certain it becomes.

Fossil Evidence

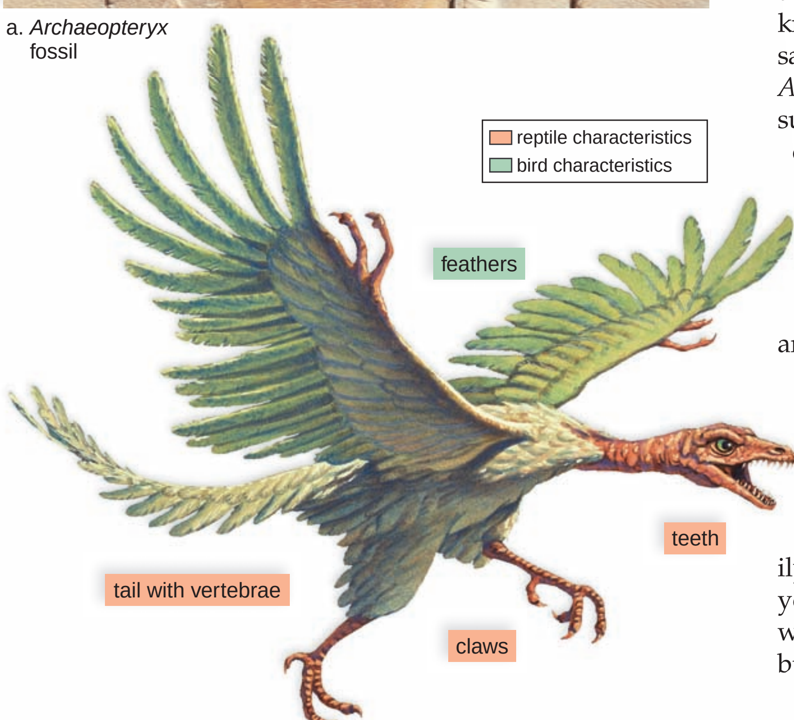
Fossils (L. *fossilis*, dug up) are the remains and traces of past life or any other direct evidence of past life. Traces include trails, footprints, burrows, worm casts, or even preserved droppings. Usually when an organism dies, the soft parts are either consumed by scavengers or decomposed by bacteria. Occasionally, the organism is buried quickly and in such a way that decomposition is never completed or is completed so slowly that the soft parts leave an imprint of their structure. Most fossils, however, consist only of hard parts, such as shells, bones, or teeth, because these are usually not consumed or destroyed.

Transitional fossils are a common ancestor for two different groups of organisms, or they are closely related to the common ancestor for these groups. Transitional fossils allow us to trace the descent of organisms. Even in Darwin's day, scientists knew of *Archaeopteryx,* which is an intermediate between dinosaurs and birds (Fig. 15.12). Progressively younger fossils than *Archaeopteryx* have been found: The skeletal remains of *Sinornis* suggest it had wings that could fold against its body like those of modern birds, and its grasping feet had an opposable toe, but it still had a tail. Another fossil, *Confuciusornis*, had the first toothless beak. A third fossil, called *Iberomesornis*, had a breastbone to which powerful flight muscles could attach. Such fossils show how the species of today evolved.

It had always been thought that whales had terrestrial ancestors. Now, fossils have been discovered that support this hypothesis. *Ambulocetus natans* (meaning the walking whale that swims) was the size of a large sea lion, with broad, webbed feet on its forelimbs and hindlimbs that enabled it to both walk and swim. It also had tiny hoofs on its toes and the primitive skull and teeth of early whales (Fig. 15.13). An older fossil, *Pakicetus*, was primarily terrestrial, and yet had the dentition of an early whale. A younger fossil, *Rodhocetus*, had reduced hindlimbs that would have been no help for either walking or swimming, but may have been used for stabilization during mating.

The origin of mammals is also well documented. The synapsids, an early amniote group, gave rise to the premammals. Slowly, mammal-like fossils acquired features that enabled them to breathe and eat at the same time, a muscular diaphragm and rib cage that helped them breathe efficiently, and so forth. The earliest true mammals were shrew-sized creatures that have been unearthed in fossil beds about 200 million years old.

a. *Archaeopteryx* fossil



b.

FIGURE 15.12 Transitional fossils.

a. *Archaeopteryx* was a transitional link between dinosaurs and birds. Fossils indicate it had feathers and wings with claws, and teeth. Most likely, it was a poor flier. **b.** *Archaeopteryx* also had a feather-covered, bony reptilian-type tail that shows up well in this artist's representation. (Orange labels = reptilian characteristics; green label = bird characteristic.)

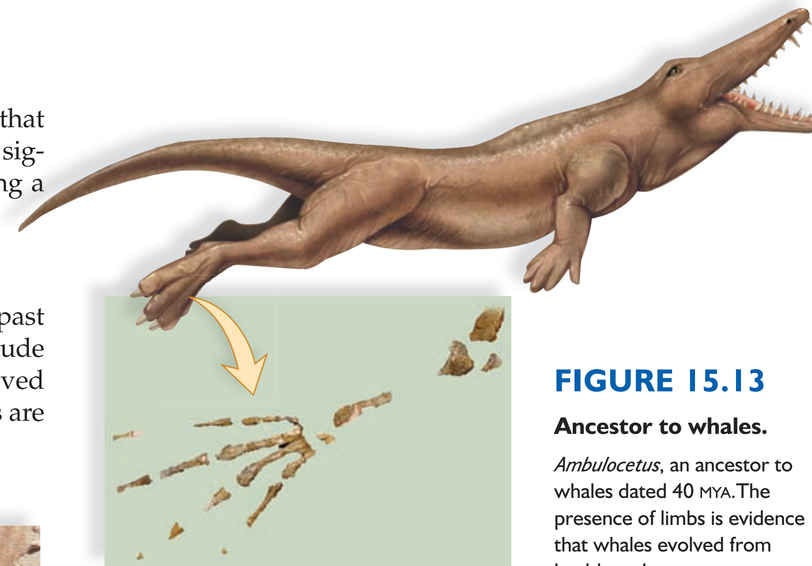


FIGURE 15.13

Ancestor to whales.

Ambulocetus, an ancestor to whales dated 40 MYA. The presence of limbs is evidence that whales evolved from land-based ancestors.

Biogeographical Evidence

Biogeography is the study of the range and distribution of plants and animals in different places throughout the world. Such distributions are consistent with the hypothesis that, when forms are related, they evolved in one locale and then spread to accessible regions. Therefore, a different mix of plants and animals would be expected whenever geography separates continents, islands, seas, and so on. As previously mentioned, Darwin noted that South America lacked rabbits, even though the environment was quite suitable to them. He concluded there are no rabbits in South America because rabbits evolved somewhere else and had no means of reaching South America.

To take another example, both cacti and spurges (*Euphorbia*) are plants adapted to a hot, dry environment—both are succulent, spiny, flowering plants. Why do cacti grow in the American deserts and most *Euphorbia* grow in African deserts when each would do well on the other continent? It seems obvious that they just happened to evolve on their respective continents.

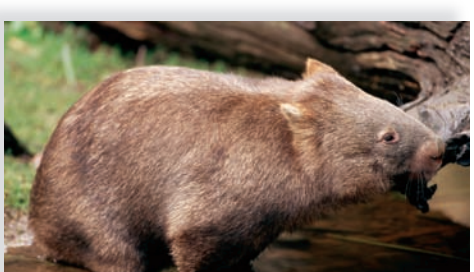
The islands of the world have many unique species of animals and plants that are found no place else, even when the soil and climate are the same. Why do so many species of finches live on the Galápagos Islands when these same species are not on the mainland? The reasonable explanation is that an ancestral finch originally inhabited the different islands. Geographic isolation allowed the ancestral finch to adapt and evolve into a different species on each island.

Also, in the history of the Earth, South America, Antarctica, and Australia were originally connected (see Fig. 18.15). Marsupials (pouched mammals) had evolved from their egg-laying mammalian ancestors at this time and today are found in both South America and Australia. But when Australia separated and drifted away, the marsupials diversified into many different forms suited to various environments of Australia (Fig. 15.14). They were free to do so because there were few, if any, placental mammals with which to compete in Australia. In South America, where there are placental mammals, marsupials are not as diverse. This supports the hypothesis that evolution is influenced by the mix of plants and animals in a particular continent—that is, by biogeography, not by design.

FIGURE 15.14 Biogeography.

Each type of marsupial in Australia is adapted to a different way of life. All of the marsupials in Australia presumably evolved from a common ancestor that entered Australia some 60 million years ago.

Sugar glider, *Petaurus breviceps*, is a tree-dweller and resembles the placental flying squirrel.



The Australian wombat, *Vombatus*, is nocturnal and lives in burrows. It resembles the placental woodchuck.

Kangaroo, *Macropus*, is an herbivore that inhabits plains and forests. It resembles the placental Patagonian cavy of South America.

Tasmanian wolf, *Thylacinus*, now extinct, was a nocturnal carnivore that inhabited deserts and plains. It resembles the placental grey wolf.

The Australian native cat, *Dasyurus*, is a carnivore and inhabits forests. It resembles the placental wild cat.

Anatomical Evidence

Darwin was able to show that a common descent hypothesis offers a plausible explanation for anatomical similarities among organisms. Vertebrate forelimbs are used for flight (birds and bats), orientation during swimming (whales and seals), running (horses), climbing (arboreal lizards), or swinging from tree branches (monkeys). Yet all vertebrate forelimbs contain the same sets of bones organized in similar ways, despite their dissimilar functions (Fig. 15.15). The most plausible explanation for this unity is that this basic forelimb plan belonged to a common ancestor, and then the plan was modified independently in all of its descendents as each continued along its own evolutionary pathway. Structures that are anatomically similar because they are inherited from a common ancestor are called **homologous structures** [Gk. *homologos*, agreeing, corresponding]. In contrast, **analogous structures** serve the same function, but they are not constructed similarly, nor do they share a common ancestry. The wings of birds and the adaptive streamline shape of a fish and squid are analogous to each other. The presence of homology, not analogy, is evidence that organisms are related.

Vestigial structures [L. *vestigium*, trace, footprint] are anatomical features that are fully developed in one group of organisms but are reduced and may have no function in similar groups. Most birds, for example, have well-developed wings used for flight. Some bird species (e.g., ostrich), however, have greatly reduced wings and do not fly. Similarly, snakes and whales, too, have no use for hindlimbs, and yet some have remnants of a pelvic girdle and legs. Humans have a tailbone but no tail. The presence of vestigial structures can be explained by the common descent hypothesis. Vestigial structures occur because organisms inherit their anatomy from their ancestors; they are traces of an organism's evolutionary history.

The homology shared by vertebrates extends to their embryological development (Fig. 15.16). At some time during development, all vertebrates have a postanal tail and exhibit paired pharyngeal pouches supported by cartilaginous arches. In fishes and amphibian larvae, these pouches develop into functioning gills. In humans, the first pair of pouches and arches becomes the jawbones, cavity of the middle ear, and the auditory tube. The second pair of pouches becomes the tonsils and facial muscle and nerve, while the third and fourth pairs become the thymus and parathyroid glands. Why should terrestrial vertebrates develop and then modify structures like pharyngeal pouches that have lost their original function? New structures (or structures with novel functions) can only originate by "modifying" the preexisting structures on one's ancestors. All vertebrates inherited the same developmental pattern from their original common ancestor. Each vertebrate group now has a specific set of modifications of this original ancestral pattern.

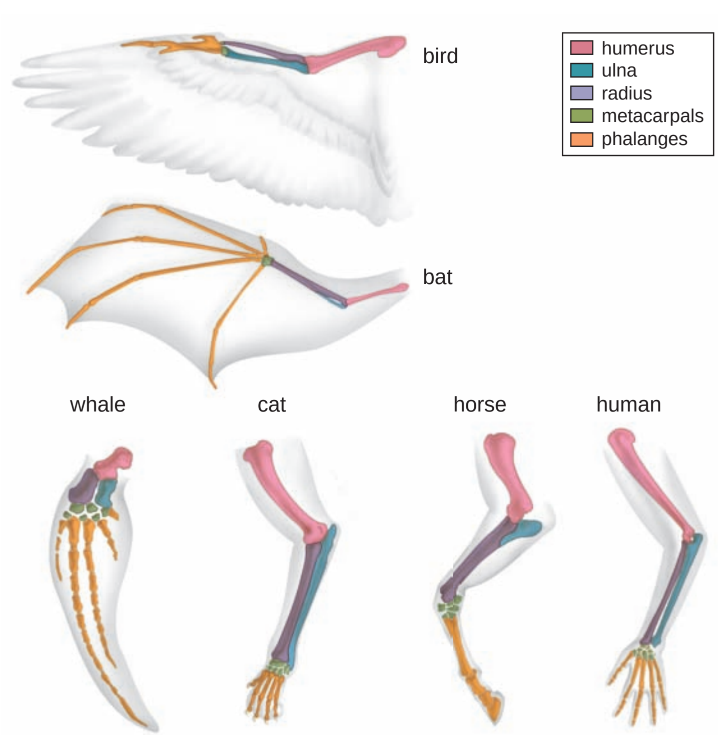


FIGURE 15.15 Significance of homologous structures.

Although the specific design details of vertebrate forelimbs are different, the same bones are present (they are color-coded). Homologous structures provide evidence of a common ancestor.

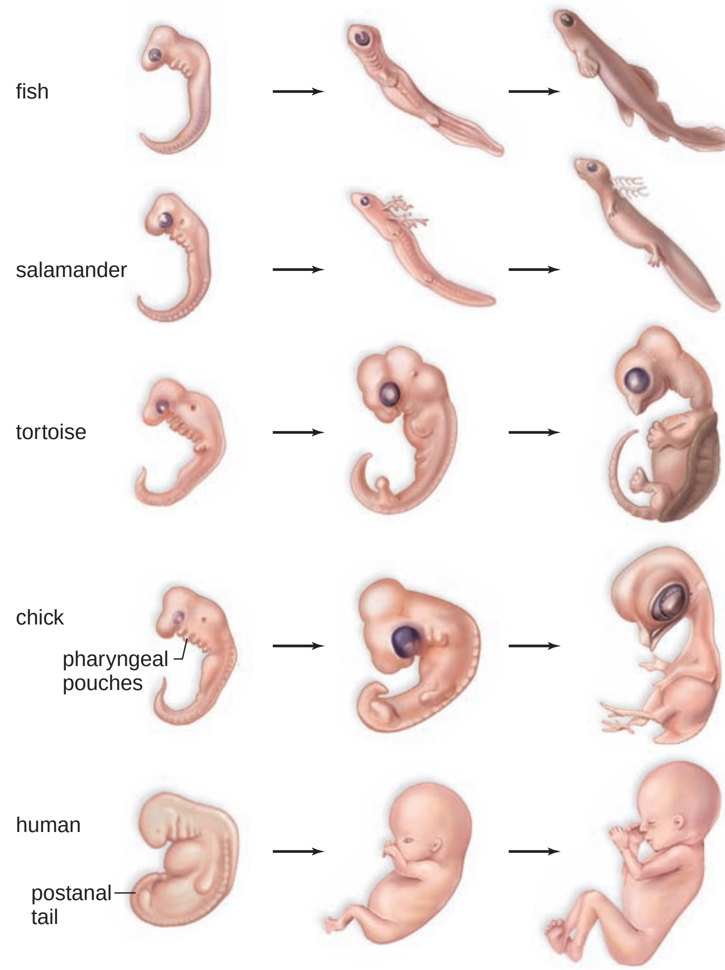


FIGURE 15.16 Significance of developmental similarities.

At these comparable developmental stages, vertebrate embryos have many features in common, which suggests they evolved from a common ancestor. (These embryos are not drawn to scale.)

Biochemical Evidence

All living organisms use the same basic biochemical molecules, including DNA (deoxyribonucleic acid), RNA (ribonucleic acid), and ATP (adenosine triphosphate). The conclusion is that these molecules were present in the first living cell or cells and have been passed on as life began.

Further, organisms use the same DNA triplet code and the same 20 amino acids in their proteins. Since the sequences of DNA bases in the genomes of many organisms are now known, it has become clear that humans share a large number of genes with much simpler organisms, even prokaryotes. This means that humans and prokaryotes also share many of the same enzymes since genes code for enzymes. Today it is possible to put a human gene in a bacterium, and it will produce a product as if it were in a human cell.

Also of interest, evolutionists who study development have found that many developmental genes are shared in animals ranging from worms to humans. It appears that life's vast diversity has come about by slight differences in genes—perhaps regulatory genes that affect the activity of other genes. The result has been widely divergent types of bodies. For example, a similar gene in arthropods and vertebrates determines the dorsal-ventral axis. Although the base sequences are similar, the genes have differing effects. Therefore, in arthropods, such as fruit flies and crayfish, the nerve cord is ventral, whereas in vertebrates, such as chickens and humans, the nerve cord is dorsal. The nerve cord eventually gives rise to the spinal cord and brain.

When the degree of similarity in DNA base sequences, or the degree of similarity in amino acid sequences, of proteins is examined, the data are as expected, assuming common descent. For example, investigators made a comparative study of the sequence of amino acids in cytochrome *c*, a molecule that is used in the electron transport chain, an important metabolic process. The sequence is expected to stay nearly the same in all organisms, because if it should change greatly, so might the function of cytochrome *c*. Figure 15.17 shows the results of their study. The sequence in a human differs from that in a monkey by only one amino acid, from that in a duck by 11 amino acids, and from that in yeast by 51 amino acids. These data are consistent with other data regarding the anatomical similarities of these organisms and, therefore, their relatedness.

Evolution is no longer considered a hypothesis. It is the great unifying theory of biology. In science, the word *theory* is reserved for those conceptual schemes that are supported by a large number of observations and have not yet been found lacking. The theory of evolution has the same status in biology that the germ theory of disease has in medicine.

Check Your Progress 15.3

1. Why is fossil evidence the best evidence for evolution? Of what significance is it that fossils can be dated?
2. Why are there so many marsupials in Australia but not in South America?
3. If American cacti and African spurges were closely related, could they be used to show that biogeography supports evolution?

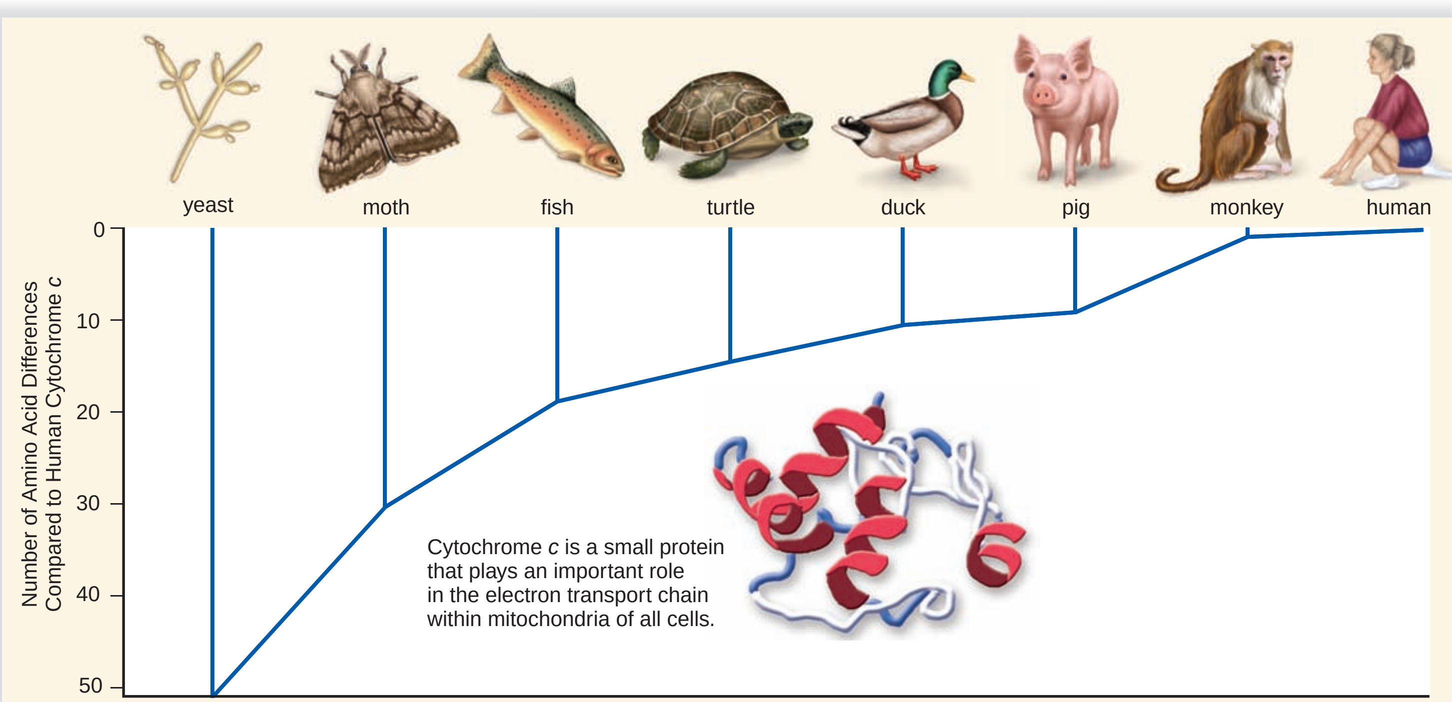


FIGURE 15.17 Significance of biochemical differences.

The branch points in this diagram indicate the number of amino acids that differ between human cytochrome *c* and the organisms depicted. These biochemical data are consistent with those provided by a study of the fossil record and comparative anatomy.

Connecting the Concepts

Before the 1800s, most people believed that each species had been created at the beginning of the world, and that modern organisms were essentially unchanged descendants of their ancestors.

At the time Charles Darwin boarded the HMS *Beagle*, he had studied the writings of his grandfather Erasmus Darwin, James Hutton, Charles Lyell, Jean-Baptiste de Lamarck, Thomas Malthus, Carolus Linnaeus, and other original thinkers. He had ample time during his five-year voyage to reflect on the ideas of these authors, and from them collectively, he built a framework that helped support his theory of descent with modification.

One aspect of scientific genius is the power of astute observation—to see what others miss or fail to appreciate. In this area, Darwin excelled. By the time he reached the Galápagos Islands, Darwin had already begun to hypothesize that species could be modified according to the environment. In other words, like other scientists, Darwin used a testable hypothesis to explain his observations. His observation of the finches on the isolated Galápagos Islands supported his hypothesis. He concluded that the finches on each island varied from one another and from mainland finches because each species had become adapted to a different habitat; therefore, one species had given rise to many. The fact that Alfred Russel Wallace simultaneously proposed natural selection as an evolutionary mechanism suggests that the scientific community was ready for a new conceptual understanding of life's diversity on Earth.

The theory of evolution has quite rightly been called the grand unifying theory (GUT) of biology. Fossils, comparative anatomy and development, biogeography, and biochemical data all indicate that living things share common ancestors. Evolutionary principles help us understand why organisms are both different and alike, and why some species flourish and others die out. As the Earth's habitats change over millions of years, those individuals with the traits best adapted to new environments survive and reproduce; thus, populations change over time.

summary

15.1 History of Evolutionary Thought

In general, the pre-Darwinian worldview was different from the post-Darwinian worldview. The scientific community, however, was ready for a new worldview, and it received widespread acceptance.

A century before Darwin's trip, the classification of organisms had been a main concern of biology. Linnaeus thought that each species had a place in the *scala naturae* and that classification should describe the fixed features of species. Some naturalists, such as Count Buffon and Erasmus Darwin, put forth tentative suggestions that species do change over time.

Georges Cuvier and Jean-Baptiste de Lamarck, contemporaries of Darwin in the late-eighteenth century, differed sharply on evolution. To explain the fossil record of a region, Cuvier proposed that a whole series of catastrophes (extinctions) and repopulations from other regions had occurred. Lamarck said that descent with modification does occur and that organisms do become adapted to their environments; however, he suggested the inheritance of acquired characteristics as a mechanism for evolutionary change.

15.2 Darwin's Theory of Evolution

Charles Darwin formulated hypotheses concerning evolution after taking a trip around the world as a naturalist aboard the HMS *Beagle* (1831–36). His hypotheses were that common descent does occur and that natural selection results in adaptation to the environment.

Darwin's trip involved two primary types of observations. His study of geology and fossils caused him to concur with Lyell that the observed massive geological changes were caused by slow, continuous changes. Therefore, he concluded that the Earth is old enough for descent with modification to occur.

Darwin's study of biogeography, including the animals of the Galápagos Islands, allowed him to conclude that adaptation to the environment can cause diversification, including the origin of new species.

Natural selection is the mechanism Darwin proposed for how adaptation comes about. Members of a population exhibit random, but inherited, variations. (In contrast to the previous worldview, variations are highly significant.) Relying on Malthus's ideas regarding overpopulation, Darwin stressed that there was a struggle for existence. The most-fit organisms are those possessing characteristics that allow them to acquire more resources and to survive and reproduce more than the less fit. In this way, natural selection can result in adaptation to an environment.

15.3 Evidence for Evolution

The hypothesis that organisms share a common descent is supported by many lines of evidence. The fossil record, biogeography, anatomical evidence, and biochemical evidence all support the hypothesis. The fossil record gives us the history of life in general and allows us to trace the descent of a particular group. Biogeography shows that the distribution of organisms on Earth is explainable by assuming organisms evolved in one locale. Comparing the anatomy and the development of organisms reveals a unity of plan among those that are closely related. All organisms have certain biochemical molecules in common, and any differences indicate the degree of relatedness. A hypothesis is greatly strengthened when many different lines of evidence support it.

Today, the theory of evolution is one of the great unifying theories of biology because it has been supported by so many different lines of evidence.

understanding the terms

Match the terms to these definitions:

a. ________________ Study of the global distribution of organisms.
b. ________________ Study of fossils that results in knowledge about the history of life.
c. ________________ Poorly developed body part that was complete and functional in an ancestor but is no longer functional in a descendant.
d. ________________ Organism's modification in structure, function, or behavior suitable to the environment.
e. ________________ Lamarckian explanation that organisms become adapted to their environment during their lifetime and pass on these adaptations to their offspring.

reviewing this chapter

1. In general, contrast the pre-Darwinian worldview with the post-Darwinian worldview. 266–68
2. Cite naturalists who made contributions to biology in the mid-eighteenth century, and state their understandings about evolutionary descent. 267
3. How did Cuvier explain the succession of life-forms in the Earth's strata? 268
4. What is meant by the inheritance of acquired characteristics, a hypothesis that Lamarck used to explain adaptation to the environment? 267–68
5. What were Darwin's views on geology, and what observations did he make regarding geology? 269
6. What observations did Darwin make regarding biogeography? How did these influence his conclusions about the origin of new species? 269–70
7. What are the steps of the natural selection process as proposed by Darwin? 271–73
8. Distinguish between the concepts of fitness and adaptation to the environment. 271–73
9. How do transitional fossils support common descent with modifications? Give an example. 276
10. How does biogeography support the concept of common descent? Explain why a diverse assemblage of marsupials evolved in Australia. 277
11. How does anatomical evidence support the concept of common descent? Explain why vertebrate forelimbs are similar despite different functions. 278
12. How does biochemical evidence support the concept of common descent? Explain why the sequence of amino acids in cytochrome *c* differs between two organisms. 279

testing yourself

Choose the best answer for each question.

1. Which of these pairs is mismatched?
   a. Charles Darwin—natural selection
   b. Linnaeus—classified organisms according to the *scala naturae*
   c. Cuvier—series of catastrophes explains the fossil record
   d. Lamarck—uniformitarianism
   e. All of these are correct.
2. According to the theory of inheritance of acquired characteristics,
   a. if a man loses his hand, then his children will also be missing a hand.
   b. changes in phenotype are passed on by way of the genotype to the next generation.
   c. organisms are able to bring about a change in their phenotype.
   d. evolution is striving toward improving particular traits.
   e. All of these are correct.
3. Why was it helpful to Darwin to learn that Lyell thought the Earth was very old?
   a. An old Earth has more fossils than a new Earth.
   b. It meant there was enough time for evolution to have occurred slowly.
   c. There was enough time for the same species to spread out into all continents.
   d. Darwin said that artificial selection occurs slowly.
   e. All of these are correct.
4. All the finches on the Galápagos Islands
   a. are unrelated but descended from a common ancestor.
   b. are descended from a common ancestor, and therefore related.
   c. rarely compete for the same food source.
   d. Both a and c are correct.
   e. Both b and c are correct.
5. Organisms
   a. compete with other members of their species.
   b. differ in fitness.
   c. are adapted to their environment.
   d. are related by descent from common ancestors.
   e. All of these are correct.
6. DNA nucleotide similarities between organisms
   a. indicate the degree of relatedness among organisms.
   b. may reflect phenotypic (morphological) similarities.
   c. explain why there are phenotypic similarities.
   d. are to be expected if the organisms are related due to common ancestry.
   e. All of these are correct.
7. If evolution occurs, we would expect different biogeographical regions with similar environments to
   a. all contain the same mix of plants and animals.
   b. each have its own specific mixes of plants and animals.
   c. have plants and animals with similar adaptations.
   d. have plants and animals with different adaptations.
   e. Both b and c are correct.
8. The fossil record offers direct evidence for common descent because you can
   a. see that the types of fossils change over time.
   b. sometimes find evidence of the transitional link between lineages.
   c. sometimes trace the ancestry of a particular group.
   d. trace the biological history of living things.
   e. All of these are correct.
9. Organisms such as birds and insects that are adapted to an aerial way of life
   a. will probably have homologous structures.
   b. will have similar adaptations.
   c. may very well have analogous structures.
   d. will have the same degree of fitness.
   e. Both b and c are correct.

For questions 10–17, match the evolutionary evidence in the key to the description. Choose more than one answer if correct.

KEY:

a. biogeographical evidence
b. fossil evidence
c. biochemical evidence
d. anatomical evidence
e. developmental evidence

10. It's possible to trace the evolutionary ancestry of a species.
11. Rabbits are not found in Patagonia.
12. A group of related species have homologous structures.
13. The same types of molecules are found in all living things.
14. Islands have many unique species not found elsewhere.
15. All vertebrate embryos have pharyngeal pouches.
16. More distantly related species have more amino acid differences in cytochrome *c*.
17. Transitional fossils have been found between some major groups of organisms.
18. Which of these is/are necessary to natural selection?
    a. variations
    b. differential reproduction
    c. an environmental catastrophe
    d. Both a and b are correct.
    e. All of these are correct.
19. Which of these is explained incorrectly?
    a. Organisms have variations—mutations and recombination of alleles occur.
    b. Organisms struggle to exist—the environment will support only so many of the same type of species.
    c. Organisms differ in fitness—adaptations enable some members of a species to reproduce more than other members.
    d. Individuals become adapted—individuals ever improve because of differential fitness.
    e. All of these are correct.

For questions 20–24, offer an explanation for each of these observations based on information in the section indicated. Write out your answer.

20. Transitional fossils serve as links between groups of organisms. See Fossil Evidence (page 276).
21. Cacti and spurges (*Euphorbia*) exist on different continents, but both have spiny, water-storing stems. See Biogeographical Evidence (page 277).
22. The forelimbs of vertebrates possess homologous structures (i.e., bones in the forelimbs). See Anatomical Evidence (page 278).
23. Amphibians, reptiles, birds, and mammals all have pharyngeal pouches at some time during development. See Anatomical Evidence (page 278).
24. The base sequence of DNA differs among species but yet maintains some degree of similarity. See Biochemical Evidence (page 279).

thinking scientifically

1. Mutations occur at random and increase the variation within a population for no particular purpose. Our immune system is capable of detecting and killing certain viruses. Would a virus that has a frequent rate of mutation be less or more able to avoid the immune system? Explain.
2. A cotton farmer applies a new insecticide against the boll weevil to his crop for several years. At first, the treatment was successful, but then the insecticide became ineffective and the boll weevil rebounded. Did evolution occur? Explain.

bioethical issue

Theory of Evolution

People are often confused by the terminology "theory of evolution." They believe that the word "theory" is being used in an everyday sense, such as "I have a theory about the win-loss record of the Boston Red Sox." But after studying this text, you realize that the word "theory" in science refers to a major scientific concept that has been so supported by observation and experiments that it is widely accepted by scientists as explaining many phenomena in the natural word. The theory of evolution is often referred to as the unifying theory of biology because it explains so many different aspects of living things.

Laypeople, in particular, who may misunderstand the term "theory," have been known to suggest that other theories, aside from the theory of evolution, should be taught in school to explain the diversity of life. Do you think that the curriculum of a science course should be restricted to content that is traditionally considered scientific, or do you believe that other "theories" that may not have been tested by experimentation should also be presented in a science course? If so, how and by whom? If not, why not?

Biology website

The companion website for *Biology* provides a wealth of information organized and integrated by chapter. You will find practice tests, animations, videos, and much more that will complement your learning and understanding of general biology.

http://www.mhhe.com/maderbiology10

16

How Populations Evolve

When your grandparents were young, infectious diseases, such as tuberculosis, pneumonia, and syphilis, killed thousands of people every year. Then in the 1940s, penicillin and other antibiotics were developed, and public health officials thought infectious diseases were a thing of the past. Today, however, many infections are back with a vengeance. Why? Because natural selection occurred. As with Staphylococcus aureus, *a few bacteria were resistant to penicillin. Therefore, they were selected over and over again to reproduce, until the entire population of bacteria became resistant to penicillin. A new antibiotic called methicillin became available in 1959 to treat penicillin-resistant bacterial strains, but by 1997, 40% of hospital staph infections were caused by* methicillin-resistant Staphylococcus aureus, *or MRSA. Now, community-acquired MRSA (CA-MRSA) can spread freely through the general populace, particularly when people are in close contact.*

This chapter gives the principles of evolution a genetic basis and shows how it is possible to genetically recognize when a population has undergone evolutionary changes. Evolutionary changes observed at the population level are termed microevolution.

MRSA can spread between members of a human social group.

concepts

16.1 Population Genetics

Darwin stressed that diversity exists among the members of a population. A **population** is all the members of a single species occupying a particular area at the same time. **Population genetics,** as its name implies, studies this diversity in terms of allele differences. Since Darwin was unaware of Mendel's work, he never had the opportunity to study the genetics of a population, as we will do in this chapter.

Genetic Diversity

When we consider that a population can have many subpopulations, such as those illustrated for a human population in Figure 16.1, we begin to realize that a population can have many phenotypic, and therefore genotypic, differences. Many traits in a population are controlled by polygenes, and if these multiple gene loci were to have multiple alleles, genetic diversity becomes plentiful, indeed.

Studies have been done to determine enzyme variations among members of a population. Extracted enzymes are subjected to electrophoresis, a process that separates proteins according to size and shape. The result in *Drosophila* suggests that a fly population has multiple alleles at no less than 30% of its gene loci. Similar results are the rule in all populations.

Increasingly today, instead of studying proteins, investigators go right to sequencing DNA to discover the amount of genetic diversity in a population, as in copy number variation s (see p. 260). This has also allowed them to discover various loci that exhibit **single nucleotide polymorphisms,** or **SNPs** (pronounced snips). These are DNA sequences in a species' genome that differ by a single nucleotide. To take an example of an SNP, compare ACGTACGTA to ACGTACCTA and notice that there is only a single base difference between the two sequences. Investigators would say that the SNP has two alleles, in this case, G and C. SNPs generally have two alleles.

SNPs that occur within a protein-coding DNA sequence can result in a change sequence of amino acids, but not necessarily, due to redundancy of the genetic code (see page 221). SNPs that do not result in a changed amino acid sequence may still cause regulatory differences. Therefore, SNPs are now thought to be an important source of genetic diversity in the populations of all species, including humans (Fig. 16.1).

Another interesting finding is that humans inherit patterns of base-pair differences now called haplotypes (from the terms haploid and genotype). To take an example, if a chromosome has a G rather than a C at a particular location, this change is most likely accompanied by other particular base differences near the G. Researchers are in the process of discovering the most common haplotypes among African, Asian, and European populations. They want to link haplotypes to the risk of specific illnesses, in the hope it will lead to new methods of preventing, diagnosing, and treating disease. Also, certain haplotypes may respond better than others to particular medicines, vaccines, and other treatment strategies.

FIGURE 16.1 The HapMap project.

The HapMap project compares DNA base-pair sequences among African, Asian, and European populations to discover unique base pair differences.

Microevolution

It wasn't until the 1930s that population geneticists worked out a way to describe the diversity in a population in terms of alleles, and to, thereby, develop a way to recognize when evolution had occurred. **Microevolution** pertains to evolutionary changes within a population.

In population genetics, the various alleles at all the gene loci in all individuals make up the **gene pool** of the population. It is customary to describe the gene pool of a population in terms of genotype and allele frequencies. Let's take an example based on the peppered moths we discussed in Chapter 15 (page 275). Suppose you research the literature and find that the color of peppered moths is controlled by a single set of alleles, and you decide to use the following key:

D = dark color

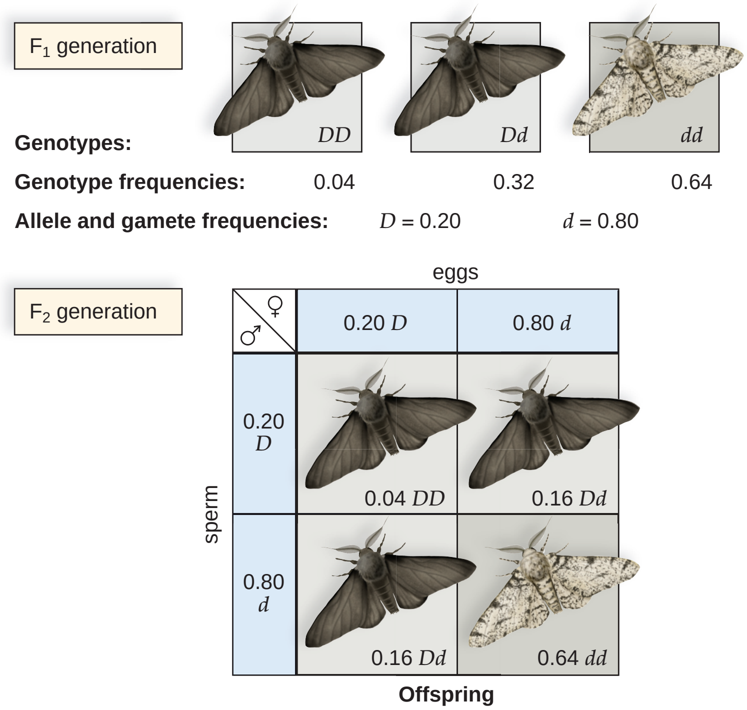
d = light color

Further, in one Great Britain population before pollution fully darkened the trees, only 4% (0.04) of moths were homozygous dominant; 32% (0.32) were heterozygous, and 64% (0.64) were homozygous recessive. From these genotype frequencies, you can calculate the allele and gamete frequencies in the populations:

genotypes	*DD*	*Dd*	*dd*
frequency of genotypes in the population	0.04	0.32	0.64
frequency of alleles and gametes in the population	0.04 + 0.16 → 0.20 *D*		0.16 + 0.64 → 0.80 *d*

The frequency of the gametes (sperm and egg) produced by this population will necessarily be the same as the allele frequencies. Assuming random mating (all possible gametes have an equal chance to combine with any other), we can use these gamete frequencies to calculate the ratio of genotypes in the next generation by using a Punnett square (Fig. 16.2).

There is an important difference between a Punnett square used for a cross between individuals, as we have done previously, and the one shown in Figure 16.2. In Figure 16.2, we are using the gamete frequencies in the population to determine the genotype frequencies in the next generation. As you can see, the genotype frequencies (and therefore the allele frequencies) in the next generation are the same as they were in the previous generation. In other words, we will find that the homozygous dominant moths are still 0.04; the heterozygous moths are still 0.32; and the homozygous recessive moths are still 0.64. This is an amazing finding, and it tells us that: *Sexual reproduction alone cannot bring about a change in genotype and allele frequencies of a population.* By the way, what percentage of moths are dark-colored, and what percentage of moths are light-colored? Adding the homozygous dominant and the heterozygous moths = 36% are dark-colored, and 64% are light-colored.



Genotype frequencies: 0.04 *DD* + 0.32 *Dd* + 0.64 *dd* = 1

$p^2 + 2pq + q^2 = 1$

p^2 = frequency of *DD* genotype (dark-colored) = $(0.20)^2$ = 0.04

$2pq$ = frequency of *Dd* genotype (dark-colored) = 2(0.20)(0.80) = 0.32

q^2 = frequency of *dd* genotype (light-colored) = $(0.80)^2$ = 0.64

1.00

FIGURE 16.2 Hardy-Weinberg equilibrium.

Using the gamete frequencies in a population, it is possible to use a Punnett square to calculate the genotype frequencies of the next generation. When this is done, it can be shown that sexual reproduction alone does not alter the Hardy-Weinberg equilibrium: the genotype, and therefore allele frequencies, remain the same. Notice the binomial expression is used to calculate the genotype frequencies of a population.

Also, the dominant allele need not increase from one generation to the next. Dominance does not cause an allele to become a common allele. The potential constancy, or equilibrium state, of gene pool frequencies was independently recognized in 1908 by G. H. Hardy, an English mathematician, and W. Weinberg, a German physician. They used the binomial expression to calculate the genotype and allele frequencies of a population, as illustrated beneath the Punnett square in Figure 16.2.

In the Hardy-Weinberg equation: $(p^2 + 2pq + q^2)$
p^2 = frequency of the homozygous dominant
p = frequency of the dominant allele
$2pq$ = frequency of the heterozygous genotype
q^2 = frequency of the homozygous recessive
q = frequency of the recessive allele

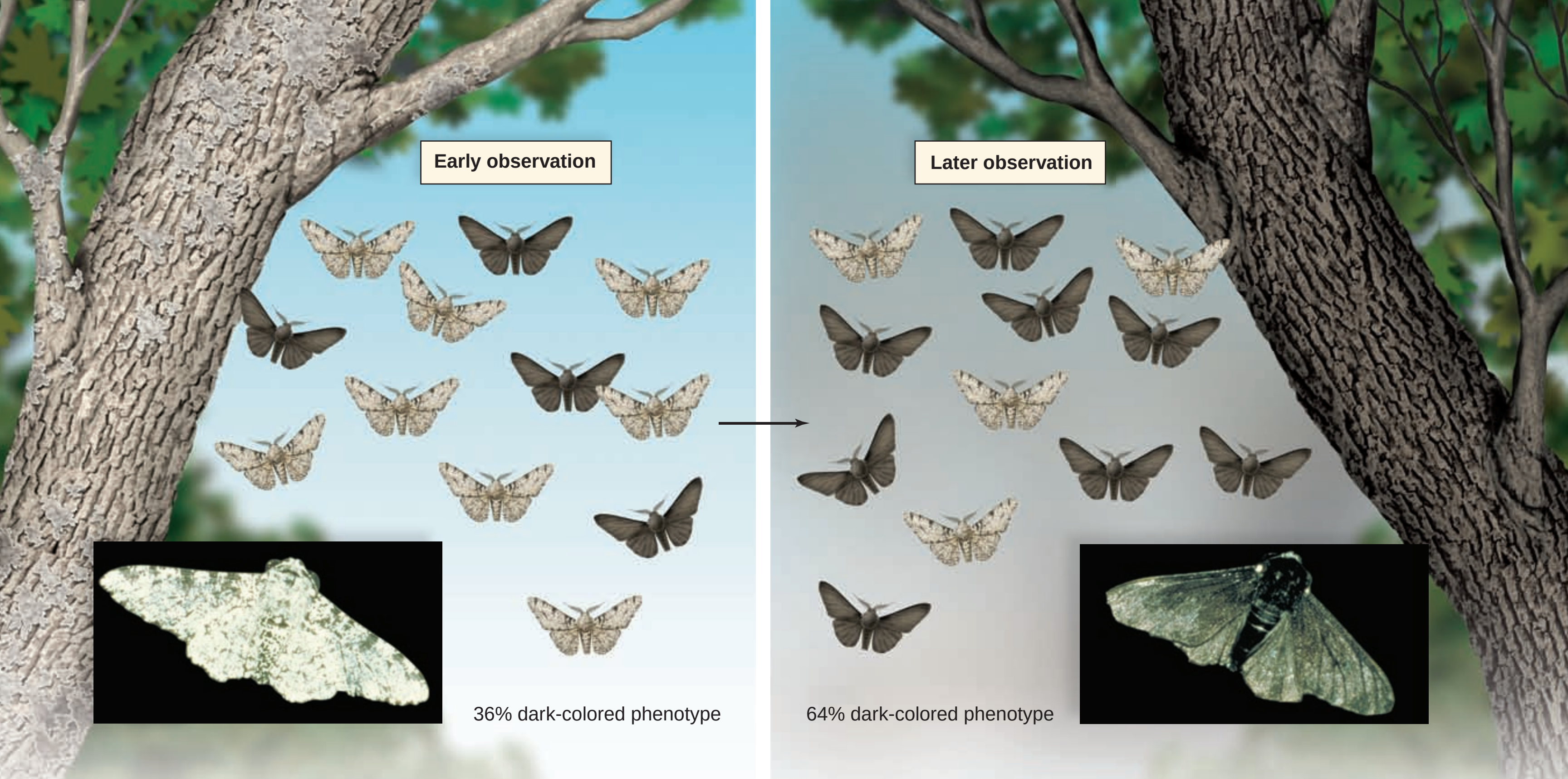


FIGURE 16.3 Microevolution.

Microevolution has occurred when there is a change in gene pool frequencies—in this case, due to natural selection. (*Left*) Light-colored moths are more frequent in the population because birds that eat moths are less likely to see light-colored peppered moths against light vegetation. (*Right*) Dark-colored moths are more frequent in the population because birds are less likely to see dark-colored moths against dark vegetation..

The **Hardy-Weinberg principle** states that an equilibrium of gene pool frequencies, calculated by using the binomial expression, will remain in effect in each succeeding generation of a sexually reproducing population, as long as five conditions are met:

1. No mutations: Allele changes do not occur, or changes in one direction are balanced by changes in the opposite direction.
2. No gene flow: Migration of alleles into or out of the population does not occur.
3. Random mating: Individuals pair by chance, not according to their genotypes or phenotypes.
4. No genetic drift: The population is very large, and changes in allele frequencies due to chance alone are insignificant.
5. No selection: Selective forces do not favor one genotype over another.

In real life, these conditions are rarely, if ever, met, and allele frequencies in the gene pool of a population do change from one generation to the next. Therefore, evolution has occurred. The significance of the Hardy-Weinberg principle is that it tells us what factors cause evolution—those that violate the conditions listed. Microevolution can be detected by noting any deviation from a Hardy-Weinberg equilibrium of allele frequencies in the gene pool of a population.

A change of allele frequencies is expected to result in a change of phenotype frequencies. Our calculation of gene pool frequencies in Figure 16.3 assumes that industrial melanism may have started but was not fully in force yet. **Industrial melanism** refers to a darkening of moths once industrialization has begun in a country. Prior to the Industrial Revolution in Great Britain, light-colored peppered moths living on the light-colored, unpolluted vegetation, were more common than dark-colored peppered moths. When dark-colored moths landed on light vegetation, they were seen and eaten by predators. In Figure 16.3, *left*, we suppose that only 36% of the population were dark-colored, while 64% were light-colored. With the advent of industry and an increase in pollution, the vegetation was stained darker. Now, light-colored moths were easy prey for birds that eat moths. Figure 16.3, *right*, shows that the gene pool frequencies switched, and now the dark-colored moths are 64% of the population. Can you calculate the change in gene pool frequencies using Figure 16.2 as a guide?

Just before the Clean Air legislation in the mid-1950s, the numbers of dark-colored moths exceeded a frequency of 80% in some populations. After the legislation, a dramatic reversal in the ratio of light-colored moths to dark-colored moths occurred once again as light-colored moths became more and more frequent. Aside from showing that natural selection can occur within a short period of time, our example shows that a change in gene pool frequencies does occur as microevolution occurs. Recall that microevolution occurs below the species level.

Causes of Microevolution

The list of conditions for a Hardy-Weinberg equilibrium implies that the opposite conditions can cause evolutionary change. The conditions are mutation, nonrandom mating, gene flow, genetic drift, and natural selection. Only natural selection results in adaptation to the environment.

Mutations

The Hardy-Weinberg principle recognizes new mutations as a force that can cause the allele frequencies to change in a gene pool and cause microevolution to occur. **Mutations,** which are permanent genetic changes, are the raw material for evolutionary change because without mutations, there could be no inheritable phenotypic diversity among members of a population. The rate of mutations is generally very low—on the order of one per 100,000 cell divisions. Also, it is important to realize that evolution is not directed, meaning that no mutation arises because the organism "needs" one. For example, the mutation that causes bacteria to be resistant was already present before antibiotics appeared in the environment.

Mutations are the primary source of genetic differences among prokaryotes that reproduce asexually. Generation time is so short that many mutations can occur quickly, even though the rate is low, and since these organisms are haploid, any mutation that results in a phenotypic change is immediately tested by the environment. In diploid organisms, a recessive mutation can remain hidden and become significant only when a homozygous recessive genotype arises. The importance of recessive alleles increases if the environment is changing; it's possible that the homozygous recessive genotype could be helpful in a new environment, if not the present one. It's even possible that natural selection will maintain a recessive allele if the heterozygote has advantages. As noted on page 284, investigators now know that even SNPs can be a significant source of diversity in a population.

In sexually reproducing organisms, the process of reproduction, consisting of meiosis and fertilization, is just as important as mutation in generating phenotypic differences, because the process can bring together a new and different combination of alleles. This new combination might produce a more successful phenotype. Success, of course, is judged by the environment and evaluated by the relative number of healthy offspring an organism produces.

Nonrandom Mating and Gene Flow

Random mating occurs when individuals pair by chance. You make sure random mating occurs when you do a genetic cross on paper or in the lab, and cross all possible types of sperm with all possible types of eggs. **Nonrandom mating** occurs when certain genotypes or phenotypes mate with one another. **Assortative mating** is a type of nonrandom mating that occurs when individuals tend to mate with those having the *same* phenotype with respect to a certain characteristic. For example, flowers such as the garden pea usually self-pollinate—therefore, the same phenotype has mated with the same phenotype (Fig. 16.4). Assortative mating can also be observed in human society. Men and women tend to marry individuals with characteristics such as intelligence and height that are similar to their own. Assortative mating causes homozygotes for certain gene loci to increase in frequency and heterozygotes for these loci to decrease in frequency.

Gene flow, also called gene migration, is the movement of alleles between populations. When animals move between populations, or when pollen is distributed between species (Fig. 16.5), gene flow has occurred. When gene flow brings a new or rare allele into the population, the allele frequency in the next generation changes. When gene flow between adjacent populations is constant, allele frequencies continue to change until an equilibrium is reached. Therefore, continued gene flow tends to make the gene pools similar and reduce the possibility of allele frequency differences between populations.

Genetic Drift

Genetic drift refers to changes in the allele frequencies of a gene pool due to chance rather than selection by the environment. Therefore, genetic drift does not necessarily result in

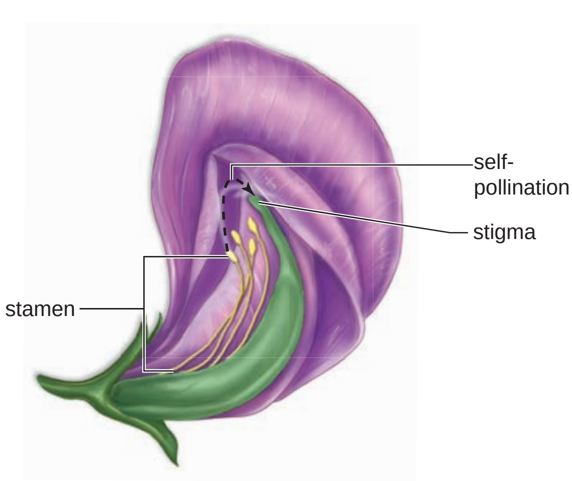


FIGURE 16.4 Anatomy of the garden pea.

The anatomy of the garden pea, *Pisum sativum,* ensures self-pollination, an example of nonrandom mating.

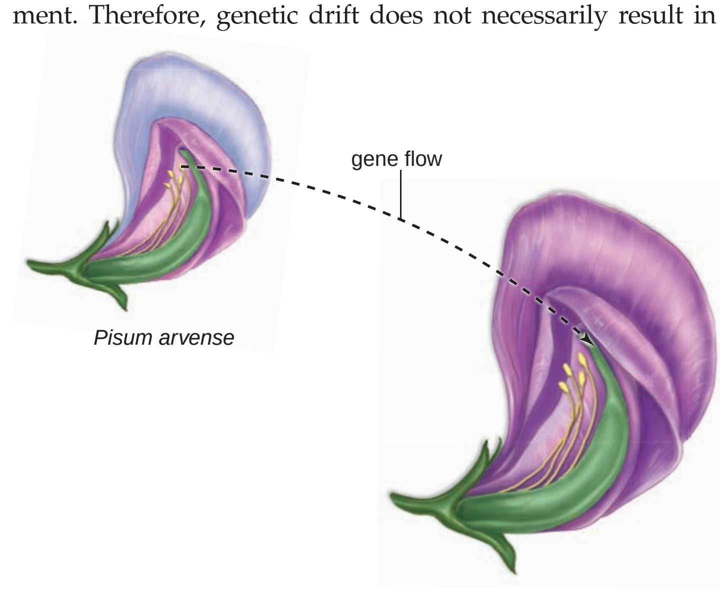


FIGURE 16.5 Gene flow.

Occasional cross-pollination between a population of *Pisum sativum* and a population of *Pisum arvense* is an example of gene flow.

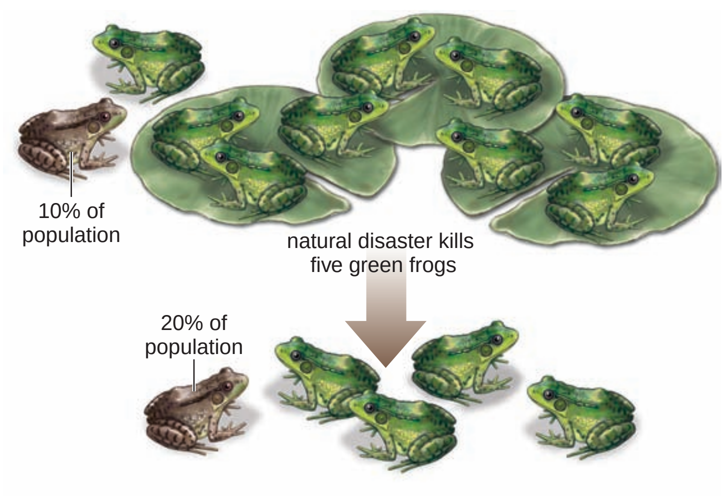


FIGURE 16.6 Genetic drift.

Genetic drift occurs when, by chance, only certain members of a population (in this case, green frogs) reproduce and pass on their alleles to the next generation. A natural disaster can cause the allele frequencies of the next generation's gene pool to be markedly different from those of the previous generation.

adaptation to the environment, as does natural selection. For example, in California, there are a number of cypress groves, each a separate population. The phenotypes within each grove are more similar to one another than they are to the phenotypes in the other groves. Some groves have conical-shaped trees, and others have pyramidally-shaped trees. The bark is rough in some colonies and smooth in others. The leaves are gray to bright green or bluish, and the cones are small or large. The environmental conditions are similar for all the groves, and no correlation has been found between phenotype and the environment across groves. Therefore, scientists hypothesize that diversity among the groves are due to genetic drift.

Although genetic drift occurs in populations of all sizes, a smaller population is more likely to show the effects of drift. Suppose the allele *B* (for brown) occurs in 10% of the members in a population of frogs. In a population of 50,000 frogs, 5,000 will have the allele *B*. If a hurricane kills off half the frogs, the frequency of allele *B* may very well remain the same among the survivors. On the other hand, 10% of a population with ten frogs means that only one frog has the allele *B*. Under these circumstances, a natural disaster could very well do away with that one frog, should half the population perish. Or, let's suppose that five green frogs only out of a ten-member population die. Now, the frequency of allele *B* will increase from 10% to 20% (Fig. 16.6).

Bottleneck and Founder Effects. When a species is subjected to near extinction because of a natural disaster (e.g., hurricane, earthquake, or fire) or because of overhunting, overharvesting, and habitat loss, it is as if most of the population has stayed behind and only a few survivors have passed through the neck of a bottle. This so-called **bottleneck effect** prevents the majority of genotypes from participating in the production of the next generation. The extreme genetic similarity found in cheetahs is believed to be due to a bottleneck effect. In a study of 47 different enzymes, each of which can come in several different forms, the sequence of amino acids in the enzymes was exactly the same in all the cheetahs. What caused the cheetah bottleneck is not known, but today they suffer from relative infertility because of the intense inbreeding that occurred after the bottleneck. Even if humans were to intervene and the population were to increase in size, without genetic variation, the cheetah could still become extinct. Other organisms pushed to the brink of extinction suffer a similar plight as the cheetah.

The **founder effect** is an example of genetic drift in which rare alleles, or combinations of alleles, occur at a higher frequency in a population isolated from the general population. Founding individuals could contain only a fraction of the total genetic diversity of the original gene pool. Which alleles the founders carry is dictated by chance alone. The Amish of Lancaster County, Pennsylvania, are an isolated group that was begun by German founders. Today, as many as 1 in 14 individuals carries a recessive allele that causes an unusual form of dwarfism (affecting only the lower arms and legs) and polydactylism (extra fingers) (Fig. 16.7). In the general population, only 1 in 1,000 individuals has this allele.

Check Your Progress 16.1

1. If two genetically different subpopulations of the same species come into contact and gene flow begins, in general, how will the genetic makeup of the merged populations change?
2. Many zoological parks send the offspring of a single breeding pair of animals to zoos around the country. How is this an example of the founder effect?

FIGURE 16.7 Founder effect.

A member of the founding population of Amish in Pennsylvania had a recessive allele for a rare kind of dwarfism linked with polydactylism. The percentage of the Amish population with this phenotype is much higher compared to that of the general population.

16.2 Natural Selection

In this chapter, we wish to consider natural selection in a genetic context. Many traits are polygenic (controlled by many genes), and the continuous variation in phenotypes results in a bell-shaped curve. When a range of phenotypes is exposed to the environment, natural selection favors the one that is most adaptive under the present environmental circumstances. Natural selection acts much the same way as a governing board that decides which applying students will be admitted to a college. Some students will be favored and allowed to enter, while others will be rejected and not allowed to enter. Of course, in the case of natural selection, the chance to reproduce is the prize awarded. In this context, natural selection can be stabilizing, directional, or disruptive (Fig. 16.8).

Stabilizing selection occurs when an intermediate phenotype can improve the adaptation of the population to those aspects of the environment that remain constant. With stabilizing selection, extreme phenotypes are selected against, and the intermediate phenotype is favored. As an example, consider that when Swiss starlings lay four to five eggs, more young survive than when the female lays more or less than this number. Genes determining physiological characteristics, such as the production of yolk, and behavioral characteristics, such as how long the female will mate, are involved in determining clutch size.

Human birth weight is another example of stabilizing selection. Through the years, hospital data have shown that human infants born with an intermediate birth weight (3–4 kg) have a better chance of survival than those at either extreme (either much less or much greater than usual). When a baby is small, its systems may not be fully functional, and when a baby is large, it may have experienced a difficult delivery. Stabilizing selection reduces the variability in birth weight in human populations (Fig. 16.9).

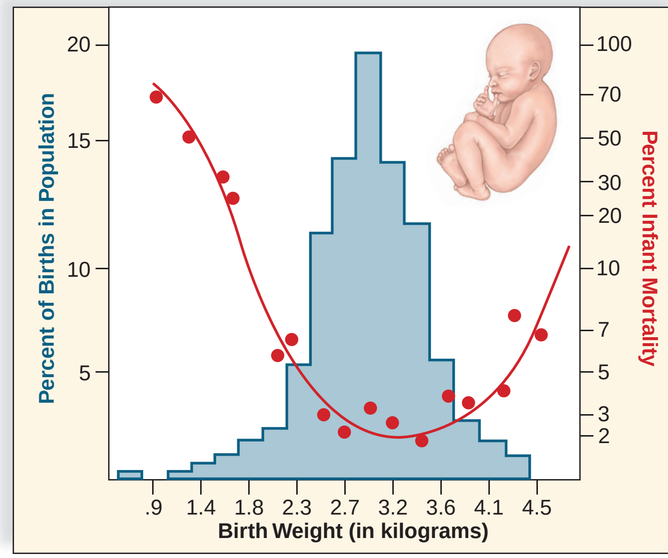


FIGURE 16.9 Human birth weight.

The birth weight (blue) is influenced by the chance of death (red).

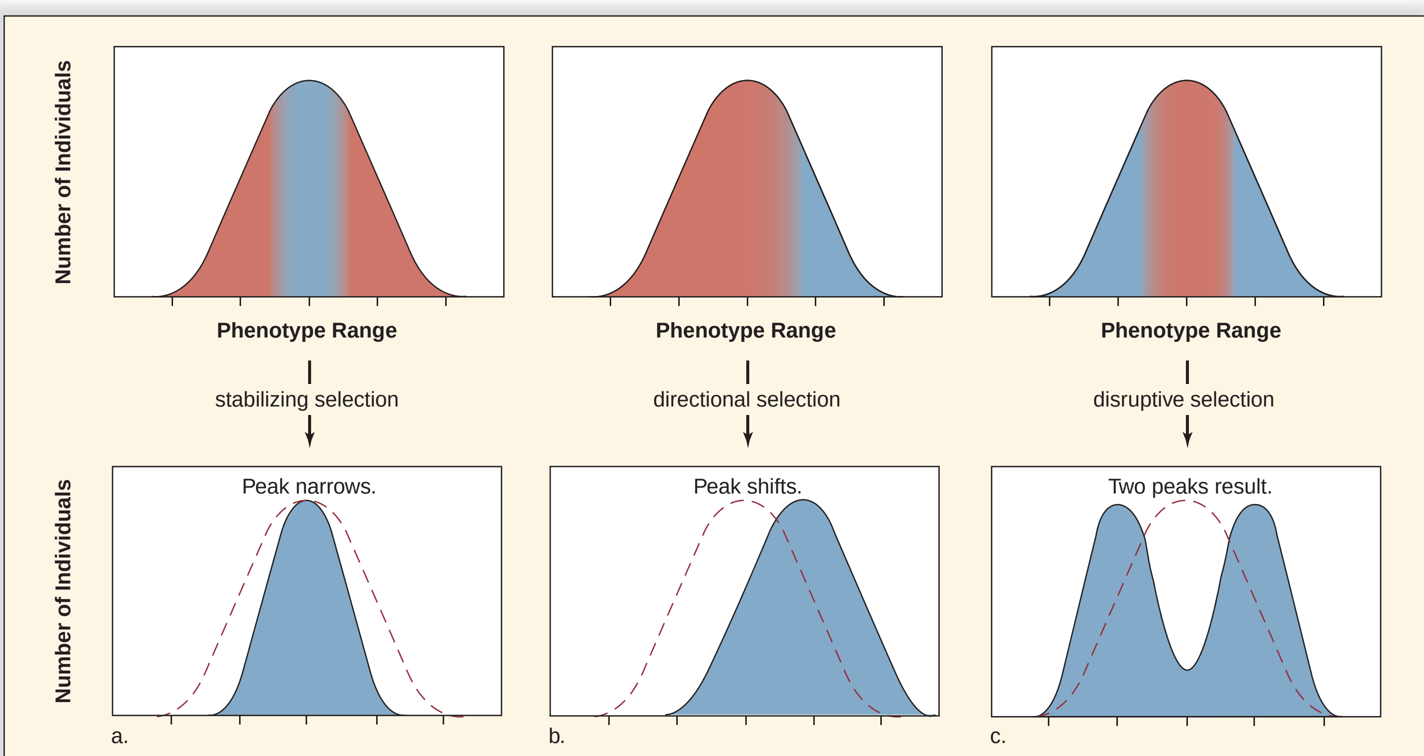
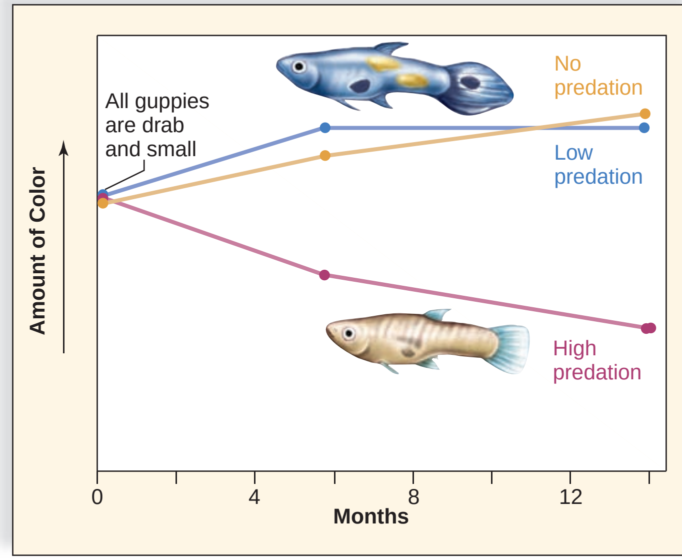


FIGURE 16.8 Three types of natural selection.

a. During stabilizing selection, the intermediate phenotype is favored; (**b**) during directional selection, an extreme phenotype is favored; and (**c**) during disruptive selection, two extreme phenotypes are favored.

Experimental site



Result

FIGURE 16.10 Directional selection.

Guppies, *Poecilia reticulata*, become more colorful (blue, yellow graph lines) in the absence of predation and less colorful (red graph line) when in the presence of predation.

Directional selection occurs when an extreme phenotype is favored, and the distribution curve shifts in that direction. Such a shift can occur when a population is adapting to a changing environment.

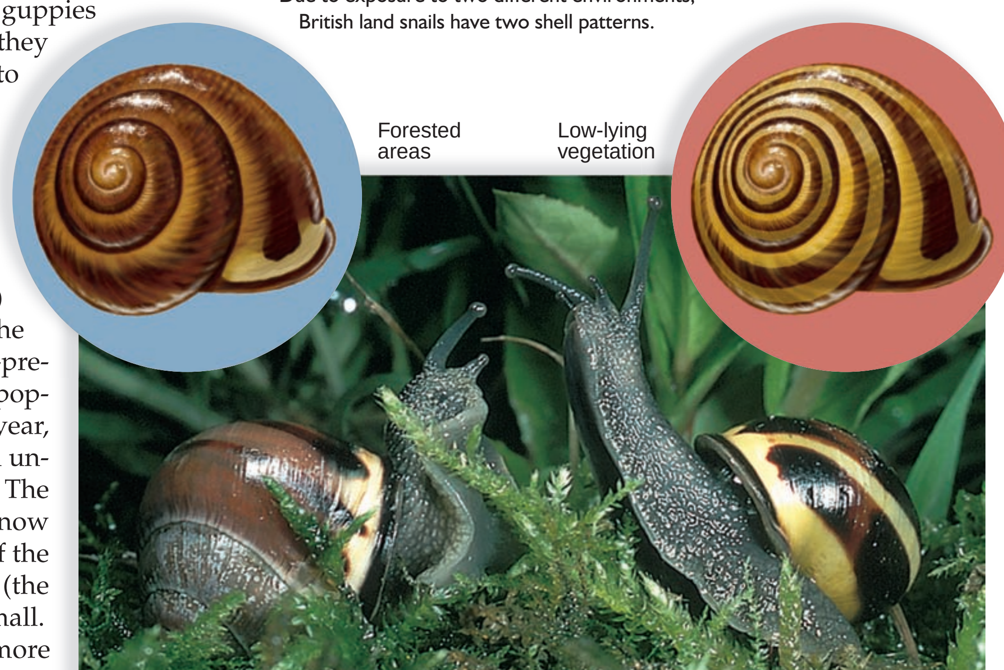
Two investigators, John Endler and David Reznick, both at the University of California, conducted a study of guppies, which are known for their bright colors and reproductive potential. These investigators noted that on the island of Trinidad, when male guppies are subjected to high predation by other fish, they tend to be drab in color and to mature early and at a smaller size. The drab color and small size are most likely protective against being found and eaten. On the other hand, when male guppies are exposed to minimal or no predation, they tend to be colorful, to mature later, and to attain a larger size.

Endler and Reznick performed many experiments, and one set is of particular interest. They took a supply of guppies from a high-predation area (below a waterfall) and placed them in a low-predation area (above a waterfall) (Fig. 16.10). The waterfall prevented the predator fish (pike) from entering the low-predation area. They monitored the guppy population for 12 months, and during that year, the guppy population above the waterfall underwent directional selection (Fig. 16.10). The male members of the population were now colorful and large in size. The members of the guppy population below the waterfall (the control population) were still drab and small.

In **disruptive selection,** two or more extreme phenotypes are favored over any intermediate phenotype. For example, British land snails have a wide habitat range that includes low-vegetation areas (grass fields and hedgerows) and forests. In forested areas, thrushes feed mainly on light-banded snails, and the snails with dark shells become more prevalent. In low-vegetation areas, thrushes feed mainly on snails with dark shells, and light-banded snails become more prevalent. Therefore, these two distinctly different phenotypes are found in the population (Fig. 16.11).

FIGURE 16.11 Disruptive selection.

Due to exposure to two different environments, British land snails have two shell patterns.



Sexual Selection

Sexual selection refers to adaptive changes in males and females that lead to an increased ability to secure a mate. Sexual selection in males may result in an increased ability to compete with other males for a mate, while females may select a male with the best **fitness** (ability to produce surviving offspring). In that way, the female increases her own fitness. Many consider sexual selection a form of natural selection because it affects fitness.

Female Choice

Females produce few eggs, so the choice of a mate becomes a serious consideration. In a study of satin bowerbirds, two opposing hypotheses regarding female choice were tested:

1. *Good genes hypothesis:* Females choose mates on the basis of traits that improve the chance of survival.
2. *Runaway hypothesis:* Females choose mates on the basis of traits that improve male appearance. The term *runaway* pertains to the possibility that the trait will be exaggerated in the male until its mating benefit is checked by the trait's unfavorable survival cost.

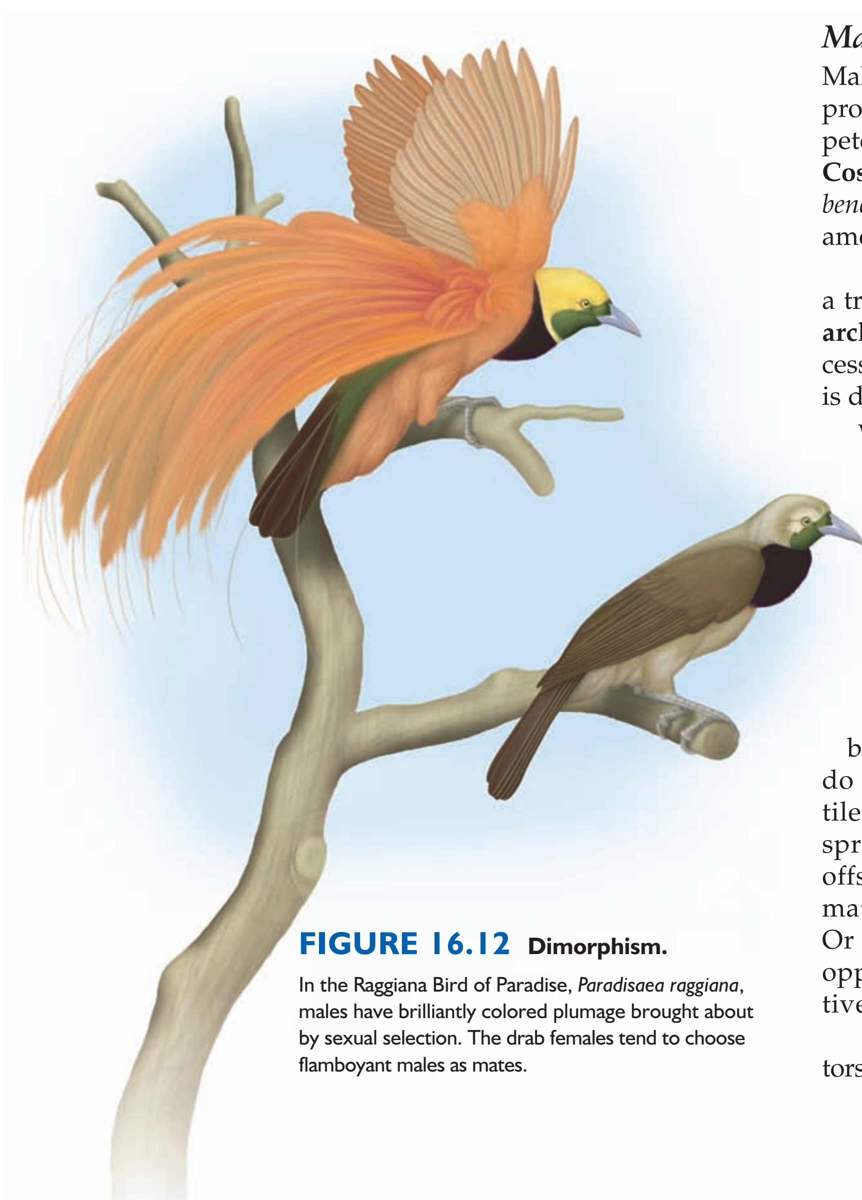


FIGURE 16.12 Dimorphism.

In the Raggiana Bird of Paradise, *Paradisaea raggiana*, males have brilliantly colored plumage brought about by sexual selection. The drab females tend to choose flamboyant males as mates.

As investigators observed the behavior of satin bowerbirds, they discovered that aggressive males were usually chosen as mates by females. It could be that inherited aggressiveness does improve the chance of survival, or it could be aggressive males are good at stealing blue feathers from other males. Females prefer blue feathers as bower decorations. Therefore, the data did not clearly support either hypothesis.

The Raggiana Bird of Paradise is remarkably *dimorphic*, meaning that males and females differ in size and other traits. The males are larger than the females and have beautiful orange flank plumes. In contrast, the females are drab (Fig. 16.12). Female choice can explain why male birds are more ornate than females. Consistent with the two hypotheses, it is possible that the remarkable plumes of the male signify health and vigor to the female. Or, it's possible that females choose the flamboyant males on the basis that their sons will have an increased chance of being selected by females. Some investigators have hypothesized that extravagant male features could indicate that they are relatively parasite-free. In barn swallows, females also choose those with the longest tails, and investigators have shown that males that are relatively free of parasites have longer tails than otherwise.

Male Competition

Males can father many offspring because they continuously produce sperm in great quantity. We expect males to compete in order to inseminate as many females as possible. **Cost-benefit analyses** have been done to determine if the *benefit* of access to mating is worth the *cost* of competition among males.

Baboons, a type of Old World monkey, live together in a troop. Males and females have separate **dominance hierarchies** in which a higher-ranking animal has greater access to resources than a lower-ranking animal. Dominance is decided by confrontations, resulting in one animal giving way to the other.

Baboons are dimorphic; the males are larger than the females, and they can threaten other members of the troop with their long, sharp canines. One or more males become dominant by frightening the other males. However, the male baboon pays a cost for his dominant position. Being larger means that he needs more food, and being willing and able to fight predators means that he may get hurt, and so forth. Is there a reproductive benefit to his behavior? Yes, in that dominant males do indeed monopolize females when they are most fertile. Nevertheless, there may be other ways to father offspring. A male may act as a helper to a female and her offspring; then, the next time she is in estrus, she may mate preferentially with him instead of a dominant male. Or subordinate males may form a friendship group that opposes a dominant male, making him give up a receptive female.

A **territory** is an area that is defended against competitors. Scientists are able to track an animal in the wild in order

FIGURE 16.13
A male olive baboon displaying full threat.

In olive baboons, *Papio anubis*, males are larger than females and have enlarged canines. Competition between males establishes a dominance hierarchy for the distribution of resources.

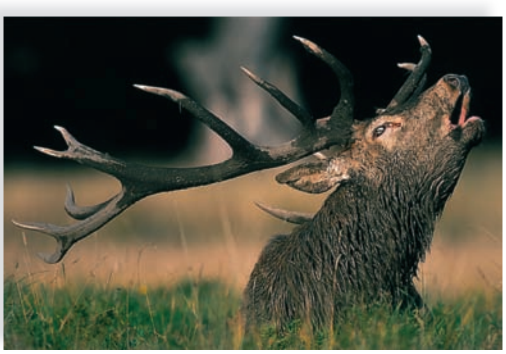
to determine its home range or territory. **Territoriality** includes the type of defensive behavior needed to defend a territory. Baboons travel within a home range, foraging for food each day and sleeping in trees at night. Dominant males decide where and when the troop will move. If the troop is threatened, dominant males protect the troop as it retreats and attack intruders when necessary. Vocalization and displays, rather than outright fighting, may be sufficient to defend a territory (Fig. 16.13). In songbirds, for example, males use singing to announce their willingness to defend a territory. Other males of the species become reluctant to make use of the same area.

Red deer stags (males) on the Scottish island of Rhum compete to be the harem master of a group of hinds (females) that mate only with them. The reproductive group occupies a territory that the harem master defends against other stags. Harem masters first attempt to repel challengers by roaring. If the challenger remains, the two lock antlers and push against one another (Fig. 16.14). If the challenger then withdraws, the master pursues him for a short distance, roaring the whole time. If the challenger wins, he becomes the harem master.

A harem master can father two dozen offspring at most, because he is at the peak of his fighting ability for only a short time. And there is a cost to being a harem master. Stags must be large and powerful in order to fight; therefore, they grow faster and have less body fat. During bad times, they are more likely to die of starvation, and in general, they have shorter lives. Harem master behavior will persist in the population only if its cost (reduction in the potential number of offspring because of a shorter life) is less than its benefit (increased number of offspring due to harem access).

Check Your Progress 16.2

1. The evolution of the horse from an animal adapted to living in a forest to one adapted to living on a plain is an example of what types of selection? Explain.
2. Why is sexual selection a form of natural selection?



a.

b.

FIGURE 16.14 **Competition between male red deer.**

Male red deer, *Cervus elaphus*, compete for a harem within a particular territory. **a.** Roaring alone may frighten off a challenger, but (**b**) outright fighting may be necessary, and the victor is most likely the stronger of the two animals.

science focus

Sexual Selection in Humans

A study of sexual selection among humans shows that the concepts of female choice and male competition apply to humans as well as to the animals we have been discussing. Increased fitness (ability to produce surviving offspring) again seems to be the result of sexual selection.

Human Males Compete

Consider that women, by nature, must invest more in having a child than men. After all, it takes nine months to have a child, and pregnancy is followed by lactation, when a woman may nurse her infant. Men, on the other hand, need only contribute sperm during a sex act that may require only a few minutes. The result is that men are generally more available for mating than are women. Because more men are available, they necessarily have to compete with others for the privilege of mating.

Like many other animals, humans are dimorphic. Males tend to be larger and more aggressive than females, perhaps as a result of past sexual selection by females. As in other animals, males pay a price for their physical attractiveness to females. Male humans live on the average seven years less than females do.

Females Choose

A study in modern Quebec sampled a large number of respondents on how often they had copulated with different sexual partners in the preceding year. Male mating success correlated best with income—those males who had both wealth and status were much more successful in acquiring mates than those who lacked these attributes. In this study, it would appear that females prefer to mate with a male who is wealthy and has a successful career because these men are more likely to be able to provide them with the resources they need to raise their children (Fig. 16A).

The desire of women for just certain types of men has led to the practice of polygamy in many primitive human societies and even in some modern societies. Women would rather share a husband who can provide resources than to have a one-on-one relationship with a poor man, because the resources provided by the wealthy man make it all the more certain that their children will live to reproduce. On the other hand, polygamy works for wealthy men because having more than one wife will undoubtedly increase their fitness as well. As an alternative to polygamy, modern societies stress monogamy in which the male plays a prominent role in helping to raise the children. This is another way males can raise their fitness.

Men Also Have a Choice

Just as women choose men who can provide resources, men prefer women who are most likely to present them with children. It has been shown that the "hourglass figure" so touted by men actually correlates with the best distribution of body fat for reproductive purposes! Men responding to questionnaires about their preferences in women list attributes that biologists associate with a strong immune system, good health, high estrogen levels, and especially with youthfulness. Young males prefer partners who are their own age, give or take five years, but as men age, they prefer women who are many years younger than themselves. Men can reproduce for many more years than women can. Therefore, by choosing younger women, older men increase their fitness as judged by the number of children they have (Fig. 16A).

Men, unlike women, do not have the same assurance that a child is their own. Therefore, men put a strong emphasis on having a wife who is faithful to them. Both men and women respondents to questionnaires view adultery in women as more offensive than adultery in men.

FIGURE 16A King Hussein and family.
The tendency of men to mate with fertile younger women is exemplified by King Hussein of Jordan, who was about 16 years older than his wife, Queen Noor. This photo shows some of their children, one of whom is now King Abdullah of Jordan.

FIGURE 16.15 Subspecies help maintain diversity.

Each subspecies of rat snakes represents a separate population of snakes. Each subspecies has a reservoir of alleles different from another subspecies. Because the populations are adjacent to one another, there is interbreeding, and, therefore, gene flow among the populations. This introduces alleles that may keep each subspecies from fully adapting to their particular environment.

16.3 Maintenance of Diversity

Diversity is maintained in a population for any number of reasons. Mutations still create new alleles, and sexual reproduction still recombines alleles due to meiosis and fertilization. Genetic drift also occurs, particularly in small populations, and the end result may be contrary to adaptation to the environment.

Natural Selection

The process of natural selection itself causes imperfect adaptation to the environment. First, it is important to realize that evolution doesn't start from scratch. Just as you can only bake a cake with the ingredients available to you, evolution is constrained by the available diversity. Lightweight titanium bones might benefit birds, but their bones contain calcium and other minerals the same as other reptiles. When you mix the ingredients for a cake, you probably follow the same steps taught to you by your elders. Similarly, the processes of development prevent the emergence of novel features, and therefore the wing of a bird has the same bones as those of other vertebrate forelimbs.

Imperfections are common because of necessary compromises. The success of humans is attributable to their dexterous hands, but the spine is subject to injury because the vertebrate spine was not originally designed to stand erect. A feature that evolves has a benefit that is worth the cost. For example, the benefit of freeing the hands must have been worth the cost of spinal injuries from assuming an erect posture. We should also consider that sexual selection has a reproductive benefit but not necessarily an adaptive benefit.

Second, we want to realize that the environment plays a role in maintaining diversity. It's easy to see that disruptive selection, dependent on an environment that differs widely, promotes polymorphisms in a population (see Fig. 16.11). Then, too, if a population occupies a wide range, as shown in Figure 16.15, it may have several subpopulations designated as subspecies because of recognizable differences. (Subspecies are given a third name in addition to the usual binomial name.) Each subspecies is partially adapted to its own environment and can serve as a reservoir for a different combination of alleles that flow from one group to the next when adjacent subspecies interbreed.

The environment also includes specific selecting agents that help maintain diversity. We have already seen how insectivorous birds can help maintain the frequencies of both the light-colored and dark-colored moths, depending on the color of background vegetation. Some predators have a search image that causes them to select the most common phenotype among its prey. This promotes the survival of the rare form and helps maintain variation. Or, a herbivore can oscillate in its preference for food. In Figure 15.11, we observed that the medium ground finch on the Galápagos Islands had a different-sized beak dependent on the available food supply. In times of drought, when only large seeds were available, birds with larger beaks were favored. In this case, we can clearly see that maintenance of variation among a population has survival value for the species.

Heterozygote Advantage

Heterozygote advantage occurs when the heterozygote is favored over the two homozygotes. In this way, heterozygote advantage assists the maintenance of genetic, and therefore phenotypic, diversity in future generations.

Sickle-Cell Disease

Sickle-cell disease can be a devastating condition. Patients can have severe anemia, physical weakness, poor circulation, impaired mental function, pain and high fever, rheumatism, paralysis, spleen damage, low resistance to disease, and kidney and heart failure. In these individuals, the red blood cells are sickle-shaped and tend to pile up and block flow through tiny capillaries. The condition is due to an abnormal form of hemoglobin (*Hb*), the molecule that carries oxygen in red blood cells. People with sickle-cell disease (Hb^SHb^S) tend to die early and leave few offspring, due to hemorrhaging and organ destruction. Interestingly, however, geneticists studying the distribution of sickle-cell disease in Africa have found that the recessive allele (Hb^S) has a higher frequency in regions (blue color) where the disease malaria is also prevalent (Fig. 16.16). Malaria is caused by a protozoan parasite that lives in and destroys the red blood cells of the normal homozygote (Hb^AHb^A). Individuals with this genotype also have fewer offspring, due to an early death or to debilitation caused by malaria.

Heterozygous individuals (Hb^AHb^S) have an advantage because they don't die from sickle-cell disease, and they don't die from malaria. The parasite causes any red blood cell it infects to become sickle-shaped. Sickle-shaped red blood cells lose potassium, and this causes the parasite to die. Heterozygote advantage causes all three alleles to be maintained in the population. It's as if natural selection were a store owner balancing the advantages and disadvantages of maintaining the recessive allele Hb^S in the warehouse. As long as the protozoan that causes malaria is present in the environment, it is advantageous to maintain the recessive allele.

Heterozygote advantage is also an example of stabilizing selection because the genotype Hb^AHb^S is favored over the two extreme genotypes, Hb^AHb^A and Hb^SHb^S. In the parts of Africa where malaria is common, one in five individuals is heterozygous (has sickle-cell trait) and survives malaria, while only 1 in 100 is homozygous and dies of sickle-cell disease. What happens in the United States where malaria is not prevalent? As you would expect, the frequency of the Hb^S allele is declining among African Americans because the heterozygote has no particular advantage in this country.

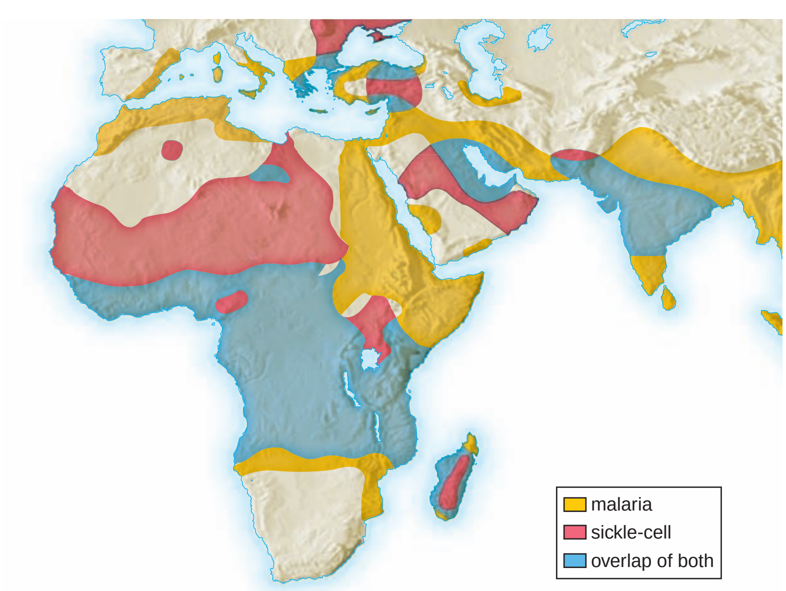


FIGURE 16.16 Sickle-cell disease.

Sickle-cell disease is more prevalent in areas of Africa where malaria is more common.

Cystic Fibrosis

Stabilizing selection is also thought to have influenced the frequency of other alleles. Cystic fibrosis is a debilitating condition that leads to lung infections and digestive difficulties. In this instance, the recessive allele, common among individuals of northwestern European descent, causes the person to have a defective plasma membrane protein. The agent that causes typhoid fever can use the normal version of this protein, but not the defective one, to enter cells. Here again, heterozygote superiority caused the recessive allele to be maintained in the population.

Check Your Progress 16.3

1. Natural selection cannot do away with diversity in a population. Explain.
2. Use a Hardy-Weinberg equilibrium to explain why heterozygote advantage maintains diversity.

Connecting the Concepts

We have seen that there are variations among the individuals in any population, whether the population is tuberculosis-causing bacteria in a city, the dandelions on a hill, or the squirrels in your neighborhood. Individuals vary because of the presence of mutations and, in sexually reproducing species, because of the recombination of alleles and chromosomes due to the processes of meiosis and fertilization.

This chapter is about microevolution—that is, gene frequency changes within a population below the level of speciation. The field of population genetics, which uses the Hardy-Weinberg principle, shows us how the study of microevolution is objective rather than subjective. A change in gene pool allele frequencies defines and signifies that microevolution has occurred. There are various agents of microevolutionary change, but only natural selection results in adaptation to the environment. Recent observations and experiments show that natural selection can occur rapidly. The emergence of MRSA, methicillin-resistant *Staphylococcus aureus* bacteria, only took about sixty years. Investigators who noted that guppies have a different appearance according to the presence of predators can also observe this change because it takes only a few months in the wild or even in the laboratory. So, we have to change our perception of natural selection as a process that cannot be observed to one that anyone can observe if they are so inclined.

Sexual selection should be considered a form of natural selection because it affects the reproductive capacity of the individual. Males that are selected to reproduce by females have more offspring than those that are not selected. Sexual selection teaches us that any trait that evolves through natural selection can be subjected to a cost-benefit analysis. It is obvious that some male traits arising through sexual selection bear a cost and may actually decrease the chance of survival. Still, if a trait helps a male leave more fertile offspring than other members of a population, it is beneficial in an evolutionary context.

We have seen that natural selection does not normally reduce variations to the point that no further evolutionary change is possible. Retention of variations is always desirable because a changing environment requires further evolutionary adjustments.

summary

16.1 Population Genetics

Microevolution requires diversity, and this chapter is interested in allele and genotype differences within a population. Diversity can even extend to SNPs, which are single nucleotide polymorphisms. Investigators are beginning to think that SNPs have significance because they may help regulate the expression of genes.

The Hardy-Weinberg equilibrium is a constancy of gene pool allele frequencies that remains from generation to generation if certain conditions are met. The conditions are no mutations, no gene flow, random mating, no genetic drift, and no selection. Since these conditions are rarely met, a change in gene pool frequencies is likely. When gene pool frequencies change, microevolution has occurred. Deviations from a Hardy-Weinberg equilibrium allow us to determine when evolution has taken place.

Mutations, gene flow, nonrandom mating, genetic drift, and natural selection all cause deviations from a Hardy-Weinberg equilibrium. Mutations are the raw material for evolutionary change. Recombination of alleles during sexual reproduction help bring about adaptive genotypes. Gene flow occurs when a breeding individual (in animals) migrates to another population or when gametes and seeds (in plants) are carried into another population. Constant gene flow between two populations causes their gene pools to become similar. Nonrandom mating occurs when relatives mate (inbreeding) or assortative mating takes place. Both of these cause an increase in homozygotes. Genetic drift occurs when allele frequencies are altered only because some individuals, by chance, contribute more alleles to the next generation. Genetic drift can cause the gene pools of two isolated populations to become dissimilar as some alleles are lost and others are fixed. Genetic drift is particularly evident after a bottleneck, when severe inbreeding occurs, or when founders start a new population.

16.2 Natural Selection

Most of the traits of evolutionary significance are polygenic; the diversity in a population results in a bell-shaped curve. Three types of selection occur: (1) directional—the curve shifts in one direction, as when bacteria become resistant to antibiotics. (New observations and experiments of late have shown how quickly directional selection can occur. Within months, guppies originally similar in appearance become more colorful if predation is absent and less colorful if predation is present.); (2) stabilizing—the peak of the curve increases, as when there is an optimum clutch size for survival of Swiss starling young; and (3) disruptive—the curve has two peaks, as when *Cepaea* snails vary because a wide geographic range causes selection to vary.

Traits that promote reproductive success are expected to be advantageous overall, despite any possible disadvantage. Males produce many sperm and are expected to compete to inseminate females. Females produce few eggs and are expected to be selective about their mates. Studies of satin bowerbirds and birds of paradise have been done to test hypotheses regarding female choice. A cost-benefit analysis can be applied to competition between males for mates, in reference to a dominance hierarchy (e.g., baboons) and territoriality (e.g., red deer).

It is possible that male competition and female choice also occur among humans. Biological differences between the sexes may promote certain mating behaviors because they increase fitness.

16.3 Maintenance of Diversity

Despite constant natural selection, genetic diversity is maintained. Mutations and recombination still occur; gene flow among small populations can introduce new alleles; and natural selection itself sometimes results in variation. In sexually reproducing diploid organisms, the heterozygote acts as a repository for recessive alleles whose frequency is low. In regard to sickle-cell disease, the heterozygote is more fit in areas where malaria occurs, and therefore both homozygotes are maintained in the population.

understanding the terms

gene flow 287
gene pool 285
genetic drift 287
Hardy-Weinberg principle 286
heterozygote advantage 295
industrial melanism 286
microevolution 285
mutation 287
nonrandom mating 287
population 284
population genetics 284
sexual selection 291
single nucleotide polymorphism (SNP) 284
stabilizing selection 289
territoriality 292
territory 291

Match the terms to these definitions:

a. ______________ Outcome of natural selection in which extreme phenotypes are eliminated and the average phenotype is conserved.

b. ______________ Marking and/or defending a particular area against invasion by another species member.

c. ______________ Change in the genetic makeup of a population due to chance (random) events; important in small populations or when only a few individuals mate.

d. ______________ Total of all the genes of all the individuals in a population.

e. ______________ Sharing of genes between two populations through interbreeding.

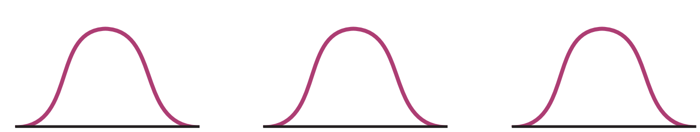
reviewing this chapter

1. The discovery of SNPs is of what significance? 284
2. What is the Hardy-Weinberg principle? 285–86
3. Name and discuss the five conditions of evolutionary change. 286–88
4. What is a population bottleneck, and what is the founder effect? Give examples of each. 288
5. Distinguish among directional, stabilizing, and disruptive selection by giving examples. 289–90
6. What is sexual selection, and why does it foster female choice and male competition during mating? 291–93
7. What is a cost-benefit analysis, and how does it apply to a dominance hierarchy and territoriality? Give examples. 291–92
8. State ways in which diversity is maintained in a population. 294–95

testing yourself

Choose the best answer for each question.

1. Assuming a Hardy-Weinberg equilibrium, 21% of a population is homozygous dominant, 50% is heterozygous, and 29% is homozygous recessive. What percentage of the next generation is predicted to be homozygous recessive?
   a. 21%
   b. 50%
   c. 29%
   d. 42%
   e. 58%
2. A human population has a higher-than-usual percentage of individuals with a genetic disorder. The most likely explanation is
   a. mutations and gene flow.
   b. mutations and natural selection.
   c. nonrandom mating and founder effect.
   d. nonrandom mating and gene flow.
   e. All of these are correct.
3. The offspring of better-adapted individuals are expected to make up a larger proportion of the next generation. The most likely explanation is
   a. mutations and nonrandom mating.
   b. gene flow and genetic drift.
   c. mutations and natural selection.
   d. mutations and genetic drift.
4. The continued occurrence of sickle-cell disease with malaria in parts of Africa is due to
   a. continual mutation.
   b. gene flow between populations.
   c. relative fitness of the heterozygote.
   d. disruptive selection.
   e. protozoan resistance to DDT.
5. Which of these is necessary to natural selection?
   a. diversity
   b. differential reproduction
   c. inheritance of differences
   d. differential adaptiveness
   e. All of these are correct.
6. When a population is small, there is a greater chance of
   a. gene flow.
   b. genetic drift.
   c. natural selection.
   d. mutations occurring.
   e. sexual selection.
7. Which of these is an example of stabilizing selection?
   a. Over time, *Equus* developed strength, intelligence, speed, and durable grinding teeth.
   b. British land snails mainly have two different phenotypes.
   c. Swiss starlings usually lay four or five eggs, thereby increasing their chances of more offspring.
   d. Drug resistance increases with each generation; the resistant bacteria survive, and the nonresistant bacteria get killed off.
   e. All of these are correct.
8. Which of these cannot occur if a population is to maintain an equilibrium of allele frequencies?
   a. People leave one country and relocate in another.
   b. A disease wipes out the majority of a herd of deer.
   c. Members of an Indian tribe only allow the two tallest people in a tribe to marry each spring.
   d. Large black rats are the preferred males in a population of rats.
   e. All of these are correct.
9. The homozygote Hb^SHb^S persists because
   a. it offers protection against malaria.
   b. the heterozygote offers protection against malaria.
   c. the genotype Hb^AHb^A offers protection against malaria.
   d. sickle-cell disease is worse than sickle-cell trait.
   e. Both b and d are correct.
10. The diagrams represent a distribution of phenotypes in a population. Superimpose another diagram on (a) to show that directional selection has occurred, on (b) to show that stabilizing selection has occurred, and on (c) to show that disruptive selection has occurred.



a. Directional selection b. Stabilizing selection c. Disruptive selection

11. The observation that the most fit male bowerbirds are the ones that can keep their nests intact supports which hypothesis?
   a. good genes hypothesis—females choose mates based on their improved chances of survival
   b. runaway hypothesis—females choose mates based on their appearance
   c. Either hypothesis could be true.
   d. Neither hypothesis is true.

12. In some bird species, the female chooses a mate that is most similar to her in size. This supports
    a. the good genes hypothesis.
    b. the runaway hypothesis.
    c. Either hypothesis could be true.
    d. Neither hypothesis is true.
13. Which of the following are costs that a dominant male baboon must pay in order to gain a reproductive benefit?
    a. He requires more food and must travel larger distances.
    b. He requires more food and must care for his young.
    c. He is more prone to injury and requires more food.
    d. He is more prone to injury and must care for his young.
    e. He must care for his young and travel larger distances.
14. A red deer harem master typically dies earlier than other males because he is
    a. likely to get expelled from the herd and cannot survive alone.
    b. more prone to disease because he interacts with so many animals.
    c. in need of more food than other males.
    d. apt to place himself between a predator and the herd to protect the herd.
15. Which one of the following statements would *not* pertain to a Punnett square that involves the alleles of a gene pool?
    a. The results tell you the chances that an offspring can have a particular condition.
    b. The results tell you the genotype frequencies of the next generation.
    c. The eggs and sperm are the gamete frequencies of the previous generation.
    d. All of these are correct.
16. Which of the following applies to the Hardy-Weinberg expression: $p^2 + 2pq + q^2$?
    a. Knowing either p^2 or q^2, you can calculate all the other frequencies.
    b. applies to Mendelian traits that are controlled by one pair of alleles
    c. $2pq$ = heterozygous individuals
    d. can be used to determine the genotype and allele frequencies of the previous and the next generations
    e. All of these are correct.
17. Following genetic drift, the
    a. genotype and allele frequencies would not change.
    b. genotype and allele frequencies would change.
    c. adaptation would occur.
    d. population would have more phenotypic variation but less genotypic variation.
18. The high frequency of Huntington disease in a population could be due to
    a. mutation plus nonrandom mating.
    b. the founder effect.
    c. natural selection because Huntington disease has a benefit.
    d. pollution in the environment.
    e. Both a and b are correct.
19. For disruptive selection to occur,
    a. the population has to contain diversity.
    b. the environment has to contain diversity.
    c. pollution must be present.
    d. natural selection must occur.
    e. All but c are correct.
20. Which of these is mismatched?
    a. male competition—males produce many sperm
    b. female choice—females produce few eggs
    c. male choice—males with exaggerated traits get to choose
    d. male competition—dominance hierarchy
21. All vertebrate forelimbs contain the same bones because
    a. they form the best structures for all sorts of adaptations.
    b. they are pliable and able to adapt.
    c. their common ancestor had these bones.
    d. vertebrates have vertebrates in their spine.
    e. All of these are correct.

additional genetics problems*

1. If $p^2 = 0.36$, what percentage of the population has the recessive phenotype, assuming a Hardy-Weinberg equilibrium?
2. If 1% of a human population has the recessive phenotype, what percentage has the dominant phenotype, assuming a Hardy-Weinberg equilibrium?
3. In a population of snails, ten had no antennae (*aa*); 180 were heterozygous with antennae (*Aa*); and 810 were homozygous with antennae (*AA*). What is the frequency of the *a* allele in the population?

*Answers to Additional Genetics Problems appear in Appendix A.

thinking scientifically

1. A farmer uses a new pesticide. He applies the pesticide as directed by the manufacturer and loses about 15% of his crop to insects. A farmer in the next state learns of these results, uses three times as much pesticide, and loses only 3% of her crop to insects. Each farmer follows this pattern for five years. At the end of five years, the first farmer is still losing about 15% of his crop to insects, but the second farmer is losing 40% of her crop to insects. How could these observations be interpreted on the basis of natural selection?
2. You are observing a grouse population in which two feather phenotypes are present in males. One is relatively dark and blends into shadows well, and the other is relatively bright and so is more obvious to predators. The females are uniformly dark-feathered. Observing the frequency of mating between females and the two types of males, you have recorded the following:
   matings with dark-feathered males: 13
   matings with bright-feathered males: 32
   Propose a hypothesis to explain why females apparently prefer bright-feathered males. What selective advantage might there be in choosing a male with alleles that make it more susceptible to predation? What data would help test your hypothesis?

Biology website

The companion website for *Biology* provides a wealth of information organized and integrated by chapter. You will find practice tests, animations, videos, and much more that will complement your learning and understanding of general biology.

http://www.mhhe.com/maderbiology10

17

Speciation and Macroevolution

the immense liger featured here is an offspring of a lion and a tiger, two normally reproductively isolated animal species. Ligers are the largest of all known cats, measuring up to 12 feet tall when standing on their hind legs and weighing as much as 1,000 lbs. Their coat color is usually tan with tiger stripes on the back and hindquarters and lion cub spots on the abdomen. A liger can produce both the "chuff" sound of a tiger and the roar of a lion. Male ligers may have a modest lion mane or no mane at all. Most ligers like to be near water and love to swim. Generally, ligers have a gentle disposition; however, considering their size and heritage, handlers should be extremely careful. By what criteria could a liger be considered a new species? Only if they, in turn, were reproductively isolated and only mated with ligers. In this chapter, we will explore the definition of a species and how species arise. In so doing, we will begin our discussion of macroevolution, which we continue in the next chapter.

This liger is a hybrid because it has a lion father and a tiger mother.

concepts

17.1 Separation of the Species

In Chapter 16, we defined microevolution as any allele frequency change within the gene pool of a population. Macroevolution, which is observed best within the fossil record, requires the origin of species, also called speciation. Speciation is the final result of changes in gene pool allelic and genotypic frequencies. The diversity of life we see about us is absolutely dependent on speciation, so it is important to be able to define a species and to know when speciation has occurred.

What Is a Species?

Up until now, we have defined a species as a type of living thing, but now we want to characterize a species in more depth. The **evolutionary species concept** recognizes that every species has its own evolutionary history, at least part of which is in the fossil record. As an example, consider that the species depicted in Figure 17.1 are a part of the evolutionary history of toothed whales. Binomial nomenclature, discussed on pages 338–39, was used to name these ancestors of whales, as well as the various species of toothed whales today. The two-part scientific name, when translated from the Latin, often tells you something about the organism. For example, the scientific name of the dinosaur, *Tyrannosaurus rex*, means "tyrant-lizard king."

The evolutionary species concept relies on identification of certain morphological (structural) traits, called diagnostic traits, to distinguish one species from another. As long as these traits are the same, fossils are considered members of the same species. Abrupt changes in these traits indicate the evolution of a new species in the fossil record. In summary, the evolutionary species concept states that members of a species share the same distinct evolutionary pathway and that species can be recognized by morphological trait differences.

One advantage of the evolutionary species concept is that it applies to both sexually and asexually reproducing organisms. A major disadvantage occurs because morphological traits are being used to distinguish species. For example, it's possible that the presence of variations, such as size differences in males and females, might make you think you are dealing with two species instead of one, and the lack of diagnostic differences could cause you to conclude that two fossils are the same species when they are not.

The evolutionary species concept necessarily assumes that the members of a species are reproductively isolated. If members of different species were to reproduce with one another—that is, hybridize—their evolutionary history would be mingled, not separate. By contrast, the **biological species concept** relies primarily on reproductive isolation rather than trait differences to define a species. In other words, although traits can help us distinguish species, the most important criterion, according to the biological species concept, is reproductive isolation—the members of a species have a single gene pool. While useful, the biological species concept cannot be applied to asexually reproducing organisms, organisms known only by the fossil record, or species that could possibly

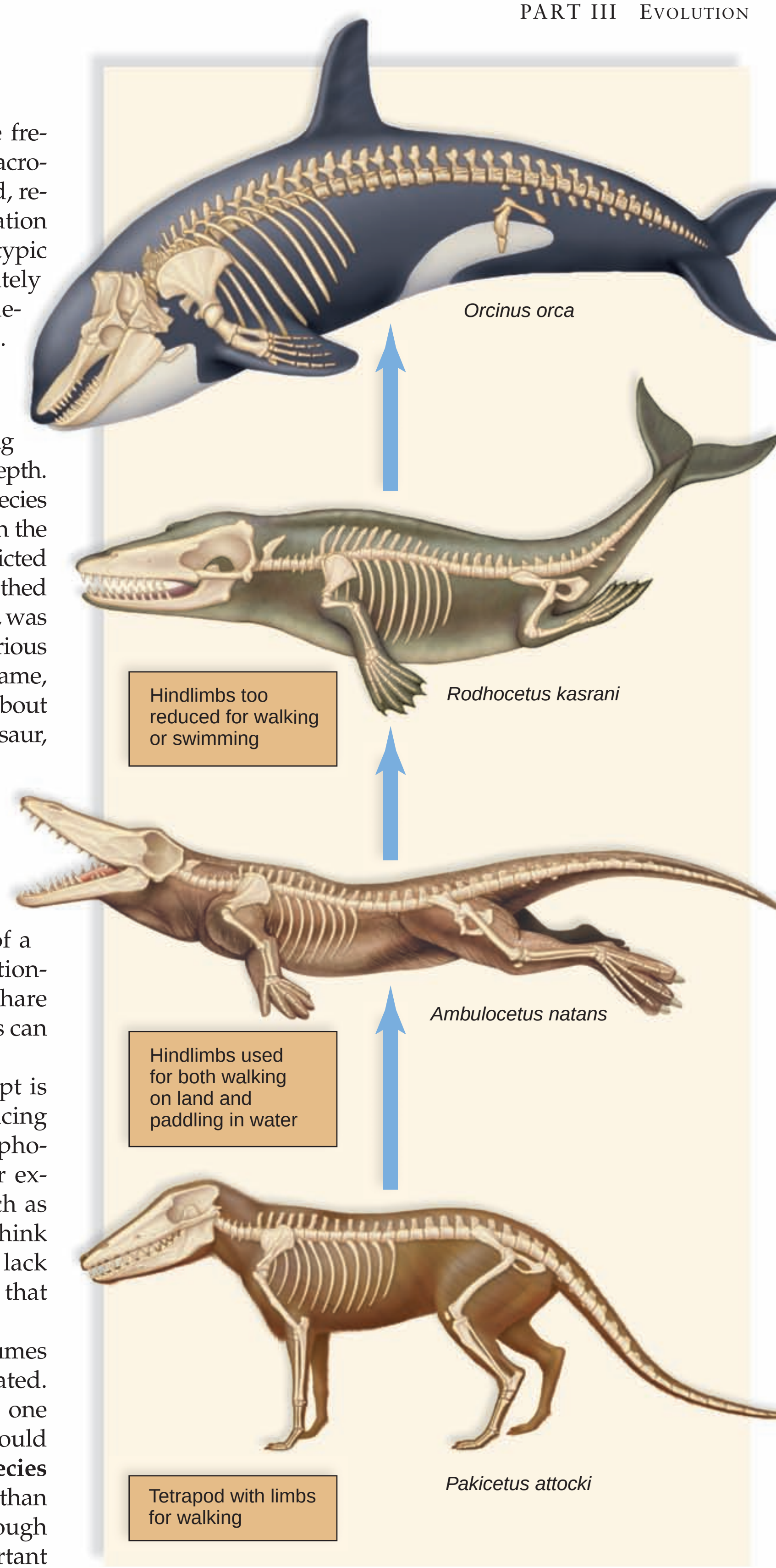
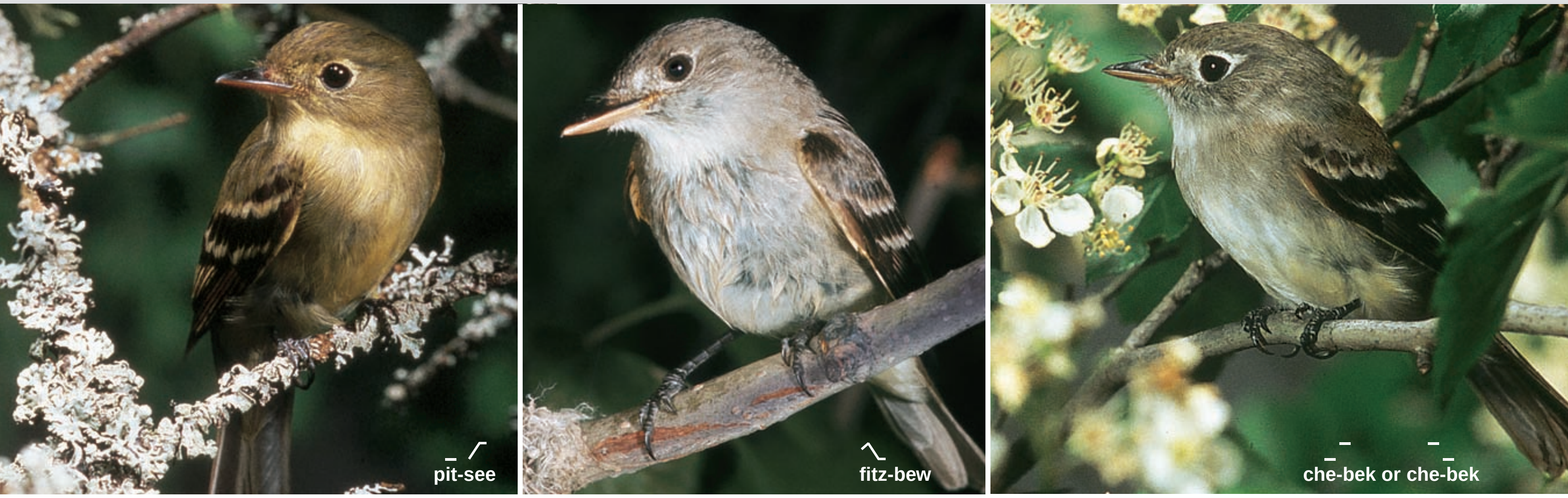


FIGURE 17.1 Evolutionary species concept.

Diagnostic traits can be used to distinguish these species known only from the fossil record. Such traits no doubt would include the anatomy of the limbs.



Acadian flycatcher, *Empidonax virescens* Willow flycatcher, *Empidonax traillii* Least flycatcher, *Empidonax minimus*

FIGURE 17.2 Biological species concept.

We know these flycatchers are separate species because they are reproductively isolated—the members of each species reproduce only with each other. Each species has a characteristic song and its own particular habitat during the mating season as well.

interbreed if they lived near one another. The benefit of the concept is that it can designate species even when trait differences may be difficult to find. Therefore, the flycatchers in Figure 17.2 are very similar, but they do not reproduce with one another; therefore, they are separate species. They live in different habitats. The Acadian flycatcher inhabits deciduous woods and wooded swamps, especially beeches; the willow flycatcher inhabits thickets, bushy pastures, old orchards, and willows; and the least flycatcher inhabits open woods, orchards, and farms. They also have different calls. Conversely, when anatomic differences are apparent, but reproduction is not deterred, only one species is present. Despite noticeable variations, humans from all over the world can reproduce with one another and belong to one species. The Massai of East Africa and the Eskimos of Alaska are kept apart by geography, but we know that, should they meet, reproduction between them would be possible (Fig. 17.3).

The biological species concept gives us a way to know when speciation has occurred, without regard to anatomic differences. As soon as descendants of a group of organisms are able to reproduce only among themselves, speciation has occurred.

In recent years, the biological species concept has been supplemented by our knowledge of molecular genetics. DNA base sequence data and differences in proteins can indicate the relatedness of groups of organisms. For example, it has recently been proposed that differences in the DNA sequence of the mitochondrial cytochrome oxidase gene could be used to identify many diverse species of animals. A study of 111 specimens of Indian mosquitoes, belonging to 15 genera and identified by morphological traits to be 63 species, was undertaken. It was found that DNA sequence differences for this gene allowed the investigators to identify 62 of the mosquito species. Two closely related species could not be identified as separate because they had negligible genetic differences.

FIGURE 17.3 Human populations.

The Massai of East Africa (*left*) and the Eskimos of Alaska (*right*) belong to the same species.

Reproductive Isolating Mechanisms

For two species to remain separate, they must be reproductively isolated—that is, gene flow must not occur between them. Reproduction, and indeed isolation, is successful when fertile offspring are produced. Only fertile offspring can pass on genes to the next generation. Reproductive barriers that prevent successful reproduction from occurring are called isolating mechanisms (Fig. 17.4) Prezygotic (before the formation of a zygote) isolating mechanisms are considered before postzygotic (after formation of a zygote) isolating mechanisms. A zygote is the first cell that results when a sperm fertilizes an egg.

Prezygotic isolating mechanisms prevent reproductive attempts or make it unlikely that fertilization will be successful if mating is attempted. These isolating mechanisms make it highly unlikely hybridization will occur.

Habitat isolation When two species occupy different habitats, even within the same geographic range, they are less likely to meet and attempt to reproduce. This is one of the reasons that the flycatchers in Figure 17.2 do not mate, and that red maple and sugar maple trees do not exchange pollen. In tropical rain forests, many animal species are restricted to a particular level of the forest canopy, and in this way they are isolated from similar species.

Temporal isolation Several related species can live in the same locale, but if each reproduces at a different time of year, they do not attempt to mate. Five species of frogs of the genus *Rana* are all found at Ithaca, New York (Fig. 17.5). The species remain separate because the period of most active mating differs and so do the breeding sites. For example, wood frogs breed in woodland ponds or shallow water, leopard frogs in lowland swamps, and pickerel frogs in streams and ponds on high ground.

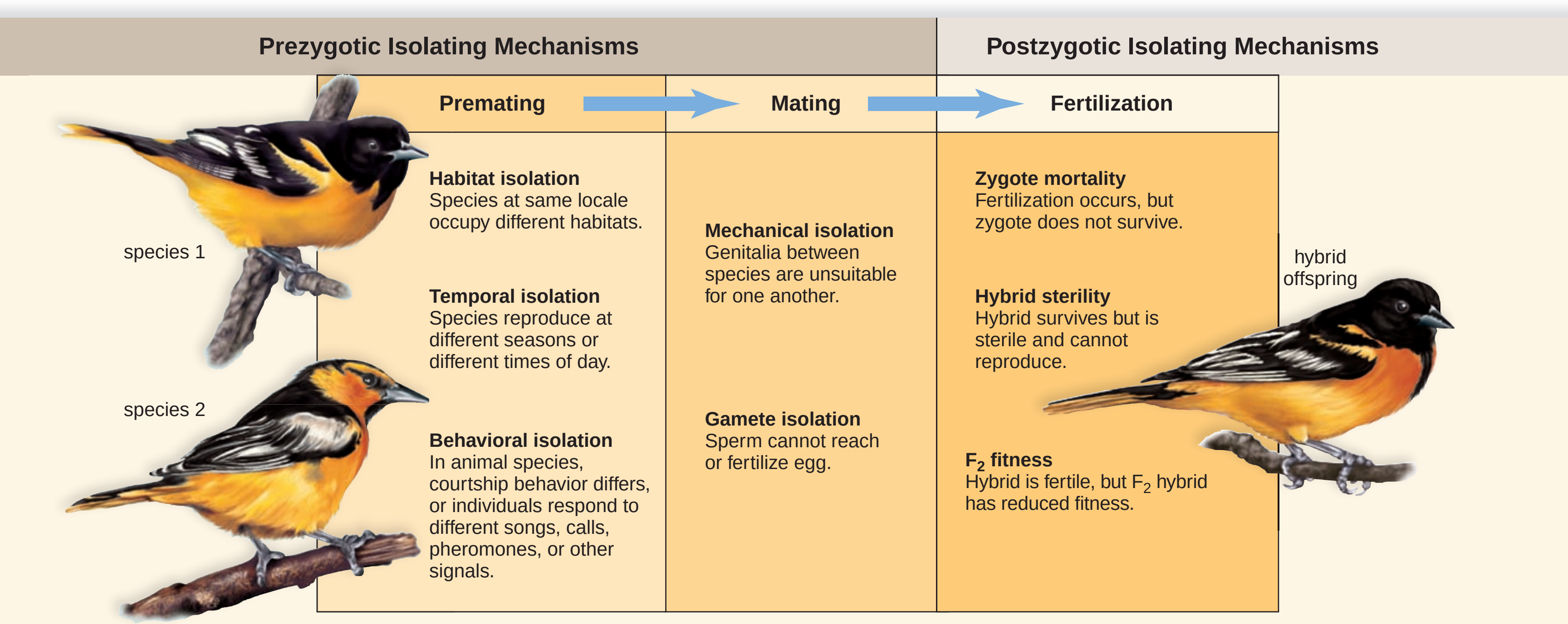
Behavioral isolation Many animal species have courtship patterns that allow males and females to recognize one another. The male blue-footed boobie in Figure 17.6 does a dance. Male fireflies are recognized by females of their species by the pattern of their flashings; similarly, female crickets recognize male crickets by their chirping. Many males recognize females of their species by sensing chemical signals called pheromones. For example, female gypsy moths release pheromones that are detected miles away by receptors on the antennae of males.

Mechanical isolation When animal genitalia or plant floral structures are incompatible, reproduction cannot occur. Inaccessibility of pollen to certain pollinators can prevent cross-fertilization in plants, and the sexes of many insect species have genitalia that do not match, or other characteristics that make mating impossible. For example, male dragonflies have claspers that are suitable for holding only the females of their own species.

Gamete isolation Even if the gametes of two different species meet, they may not fuse to become a zygote. In animals, the sperm of one species may not be able to survive in the reproductive tract of another species, or the egg may have receptors only for sperm of its species. In plants, only certain types of pollen grains can germinate so that sperm successfully reach the egg.

FIGURE 17.4 Reproductive barriers.

Prezygotic isolating mechanisms prevent mating attempts or a successful outcome should mating take place. No zygote ever forms. Postzygotic isolating mechanisms prevent the zygote from developing—or should an offspring result, it is not fertile.



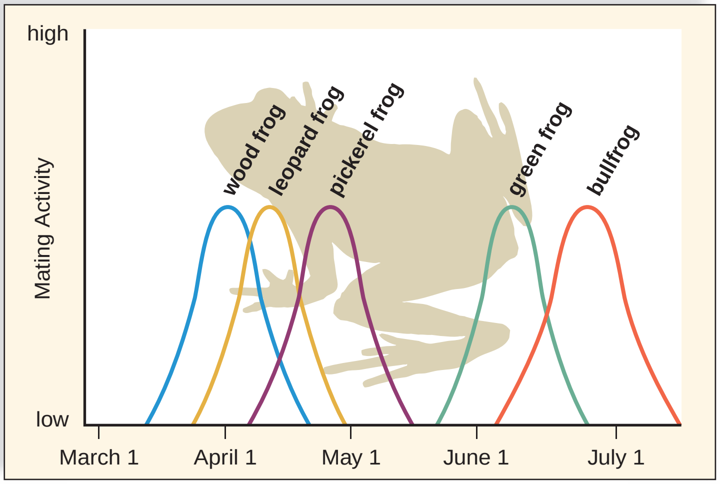


FIGURE 17.5 Temporal isolation.

Five species of frogs of the genus *Rana* are all found at Ithaca, New York. The species remain separate due to breeding peaks at different times of the year, as indicated by this graph.

FIGURE 17.6 Prezygotic isolating mechanism.

An elaborate courtship display allows the blue-footed boobies of the Galápagos Islands to select a mate. The male lifts up his feet in a ritualized manner that shows off their bright blue color.

Postzygotic (after the formation of a zygote) **isolating mechanisms** prevent hybrid offspring from developing, even if reproduction attempts have been successful. Or, if a hybrid is born, it is infertile and cannot reproduce. Either way, the genes of the parents are unable to be passed on.

Zygote mortality A hybrid zygote may not be viable, and so it dies. A zygote with two different chromosome sets may fail to go through mitosis properly, or the developing embryo may receive incompatible instructions from the maternal and paternal genes so that it cannot continue to exist.

Hybrid sterility The hybrid zygote may develop into a sterile adult. As is well known, a cross between a male horse and a female donkey produces a mule, which is usually sterile—it cannot reproduce (Fig. 17.7). Sterility of hybrids generally results from complications in meiosis that lead to an inability to produce viable gametes. Similarly, a cross between a cabbage and a radish produces offspring that cannot form gametes, most likely because the cabbage chromosomes and the radish chromosomes could not align during meiosis.

F_2 fitness Even if hybrids can reproduce, their offspring may be unable to reproduce. In some cases, mules are fertile, but their offspring (the F_2 generation) are not fertile.

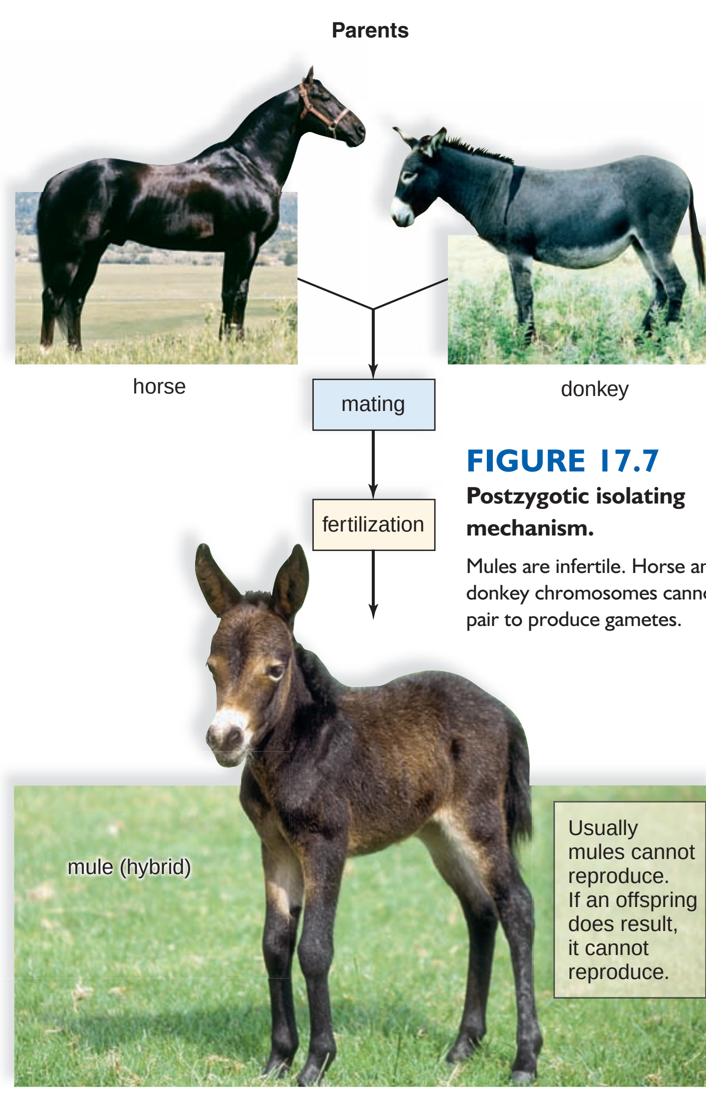


FIGURE 17.7 Postzygotic isolating mechanism.

Mules are infertile. Horse and donkey chromosomes cannot pair to produce gametes.

Check Your Progress 17.1

1. On the basis of the evolutionary species concept, should ligers be considered a species in their own right?
2. Lions and tigers do not meet in the wild, and ligers born in captivity are sterile. What (**a**) pre- and (**b**) postzygotic isolating mechanisms are working?

17.2 Modes of Speciation

Researchers recognize two modes of **speciation,** splitting of one species into two or more species or the transformation of one species into a new species over time. One requires geographic isolation and the other one does not. Geographic isolation is helpful because it allows populations to continue on their own evolutionary path, which eventually causes them to be reproductively isolated from other species. Once reproductive isolation has begun, it can be reinforced by the evolution of more traits that prevent breeding with related species. Geographic isolation can repeatedly occur, so one ancestral species can give rise to several other species.

Allopatric Speciation

In 1942, Ernst Mayr, an evolutionary biologist, published the book *Systematics and the Origin of Species*, in which he proposed the biological species concept and a process by which speciation could occur. He said that when members of a species become isolated, the new populations will start to differ because of genetic drift and natural selection over a period of time. Eventually, the two groups will be unable to mate with one another. At that time, they have evolved into new species. Mayr's hypothesis, termed **allopatric speciation** [Gk. *allo*, other, and *patri*, fatherland], requires that populations be separated by a geographic barrier for speciation to occur.

Examples of Allopatric Speciation

Figure 17.8 features an example of allopatric speciation that has been extensively studied in California. An ancestral population of *Ensatina* salamanders lives in the Pacific Northwest. (1) Members of this ancestral population migrated southward, establishing a series of populations. Each population was exposed to its own selective pressures along the coastal mountains and the Sierra Nevada mountains. (2) Due to the presence of the Central Valley of California, gene flow rarely occurs between the eastern populations and the western populations. (3) Genetic differences increased from north to south, resulting in two distinct forms of *Ensatina* salamanders in Southern California that differ dramatically in color and rarely interbreed.

Geographic isolation is even more obvious in other examples. The green iguana of South America is hypothesized to be the common ancestor for both the marine iguana on the Galápagos Islands (to the west) and the rhinoceros iguana on Hispaniola, an island to the north. If so, how could it happen? Green iguanas are strong swimmers, so by chance, a few could have migrated to these islands, where they formed populations separate from each other and from the parent population back in South America. Each population continued on its own evolutionary path as new mutations, genetic drift, and different selection pressures occurred. Eventually, reproductive isolation developed, and the result was three species of iguanas that are reproductively isolated from each other.

A more detailed example of allopatric speciation involves sockeye salmon in Washington State. In the 1930s and 1940s, hundreds of thousands of sockeye salmon were introduced into Lake Washington. Some colonized an area of the lake near Pleasure Point Beach (Fig. 17.9*a*). Others migrated into the Cedar River (Fig. 17.9*b*). Andrew Hendry, a biologist at McGill University, is able to tell a Pleasure Point Beach salmon from a Cedar River salmon because they differ in shape and size due to the demands of reproducing. In the river, where the waters are fast-moving, males tend to be more slender than those at the beach. A slender body is better able to turn sideways in a strong current, and the courtship ritual of a sockeye salmon requires this maneuver. On

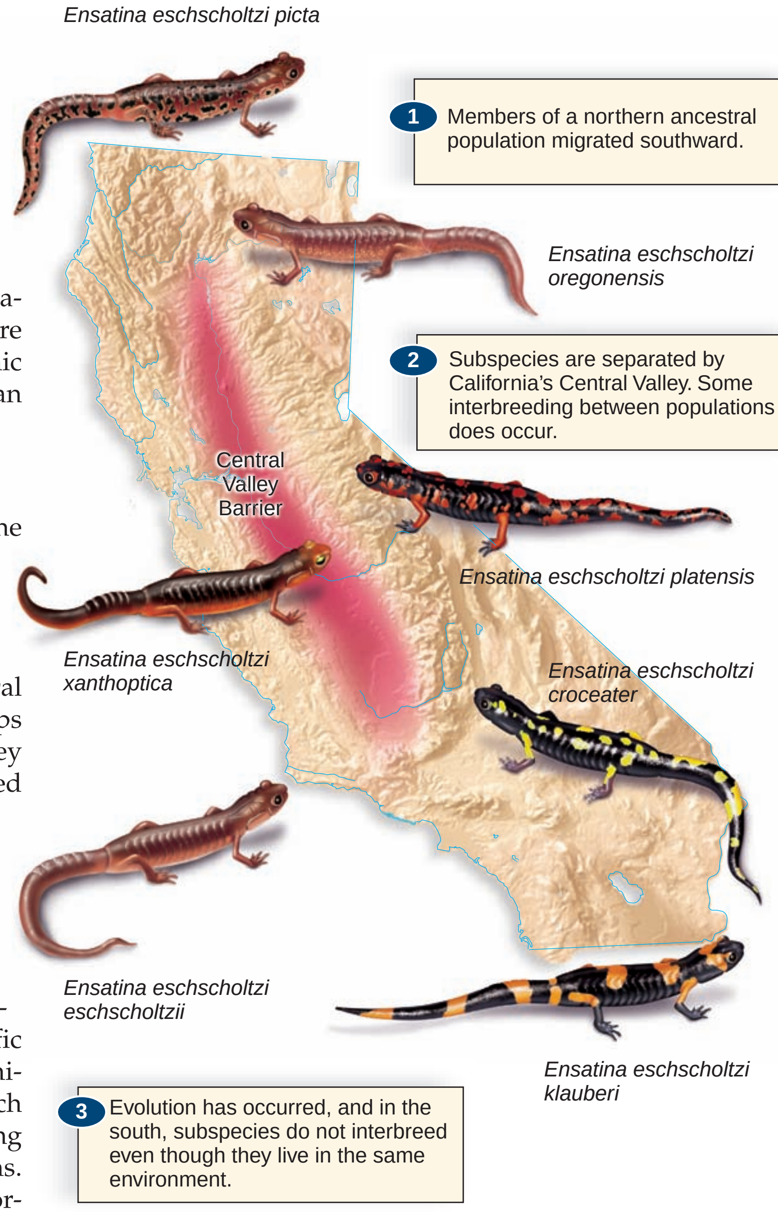
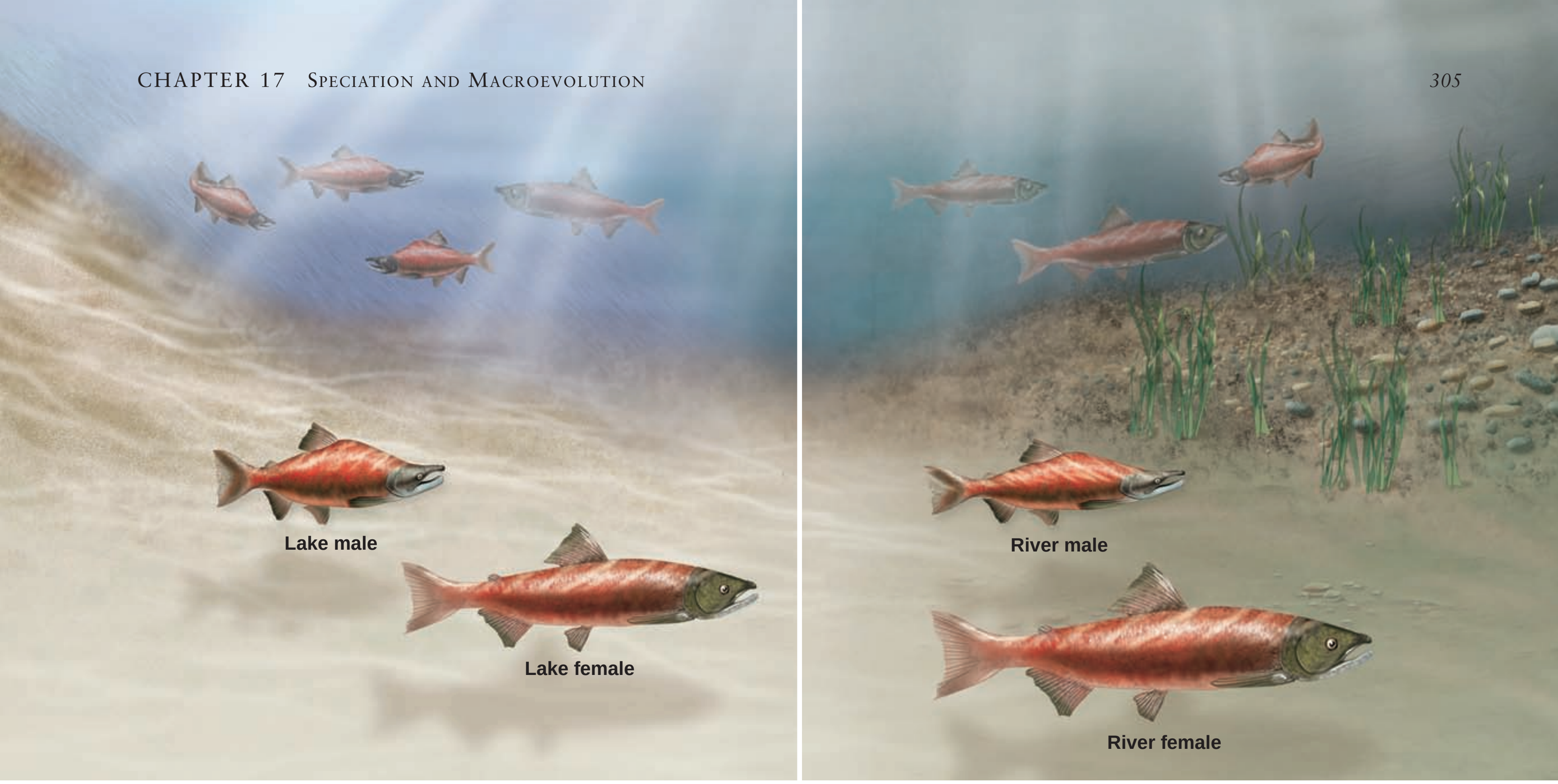


FIGURE 17.8 Allopatric speciation among *Ensatina* salamanders.

The Central Valley of California is separating a range of populations descended from the same northern ancestral species. The limited contact between the populations on the west and those on the east allows genetic changes to build up so that two populations, both living in the south, do not reproduce with one another, and therefore can be designated as separate species.



a. Sockeye salmon at Pleasure Point Beach, Lake Washington

b. Sockeye salmon in Cedar River. The river connects with Lake Washington.

FIGURE 17.9 **Allopatric speciation among sockeye salmon.**

In Lake Washington, salmon that matured (**a**) at Pleasure Point Beach do not reproduce with those that matured in (**b**) the Cedar River. The females from Cedar River are noticeably larger and the males are more slender than those from Pleasure Point Beach, and these shapes help them reproduce in the river.

the other hand, the females tend to be larger than those at the beach. This larger body helps them dig slightly deeper nests in the gravel beds on the river bottom. Deeper nests are not disturbed by river currents and remain warm enough for egg viability.

Hendry has an independent way of telling beach salmon from river salmon. Ear stones called otoliths reflect variations in water temperature while a fish embryo is developing. Water temperatures at the beach are relatively constant compared to the river temperatures. By checking otoliths in adults, Hendry found that a third of the sockeye males at Pleasure Point Beach had grown up in the river. Yet the distinction between male and female shape and size in the two locations remains. Therefore, these males are not successful breeders along the beach. In other words, reproductive isolation has occurred.

Reinforcement of Reproductive Isolation

As seen in sockeye salmon and other animals, a side effect to adaptive changes involving mating is reproductive isolation. Another example is seen among *Anolis* lizards in which males court females by extending a colorful flap of skin, called a "dewlap." The dewlap must be seen in order to attract mates. Populations of *Anolis* in a dim forest tend to evolve a light-colored dewlap, while populations in open habitats tend to evolve dark-colored ones. This change in dewlap color causes the populations to be reproductively isolated, because females distinguish males of their species by their dewlaps.

As populations become reproductively isolated, postzygotic isolating mechanisms may arise before prezygotic isolating mechanisms. As we have seen, when a horse and a mule reproduce, the hybrid or the offspring of a hybrid is not fertile. Therefore, natural selection would favor any variation in populations that prevents the occurrence of hybrids when they do not have offspring. Indeed, natural selection would favor the continual improvement of prezygotic isolating mechanisms until the two populations are completely reproductively isolated. The term reinforcement is given to the process of natural selection favoring variations that lead to reproductive isolation. An example of reinforcement has been seen in the pied and collared flycatchers of the Czech Republic and Slovakia, where both species occur in close proximity. Only here have the pied flycatchers evolved a different coat color than the collared flycatchers. The difference in color helps the two species recognize and mate with their own species.

Adaptive Radiation

Adaptive radiation is a type of allopatric speciation and occurs when a single ancestral species gives rise to a variety of species, each adapted to a specific environment. An *ecological niche* is where a species lives and how it interacts with other species.

Examples of Adaptive Radiation

When an ancestral finch arrived on the Galápagos Islands, its descendants spread out to occupy various niches. Geographic isolation of the various finch populations caused their gene pools to become isolated. Because of natural selection, each population adapted to a particular habitat on its island. In time, the many populations became so genotypically different that now, when by chance they reside on the same island, they do not interbreed, and are therefore separate species. During mating, finches use beak shape to recognize members of the same species, and suitors with the wrong type of beak are rejected.

Similarly, on the Hawaiian Islands, a wide variety of honeycreepers are descended from a common goldfinchlike ancestor that arrived from Asia or North America about 5 million years ago. Today, honeycreepers have a range of beak sizes and shapes for feeding on various food sources, including seeds, fruits, flowers, and insects (Fig. 17.10). Adaptive radiation also occurs among plants; a good example is the silversword alliance, which includes plants adapted to moist and dry environments and even lava fields.

Adaptive radiation has occurred throughout the history of life on Earth when a group of organisms exploits new environments. For example, with the demise of the dinosaurs about 66 million years ago, mammals underwent adaptive radiation as they exploited environments previously occupied by the dinosaurs. Mammals diversified in just 10 million years to include the early representatives of all the mammalian orders, including hoofed mammals (e.g., horses and pigs), aquatic mammals (e.g., whales and seals), primates (e.g., lemurs and monkeys), flying mammals (e.g., bats), and rodents (e.g., mice and

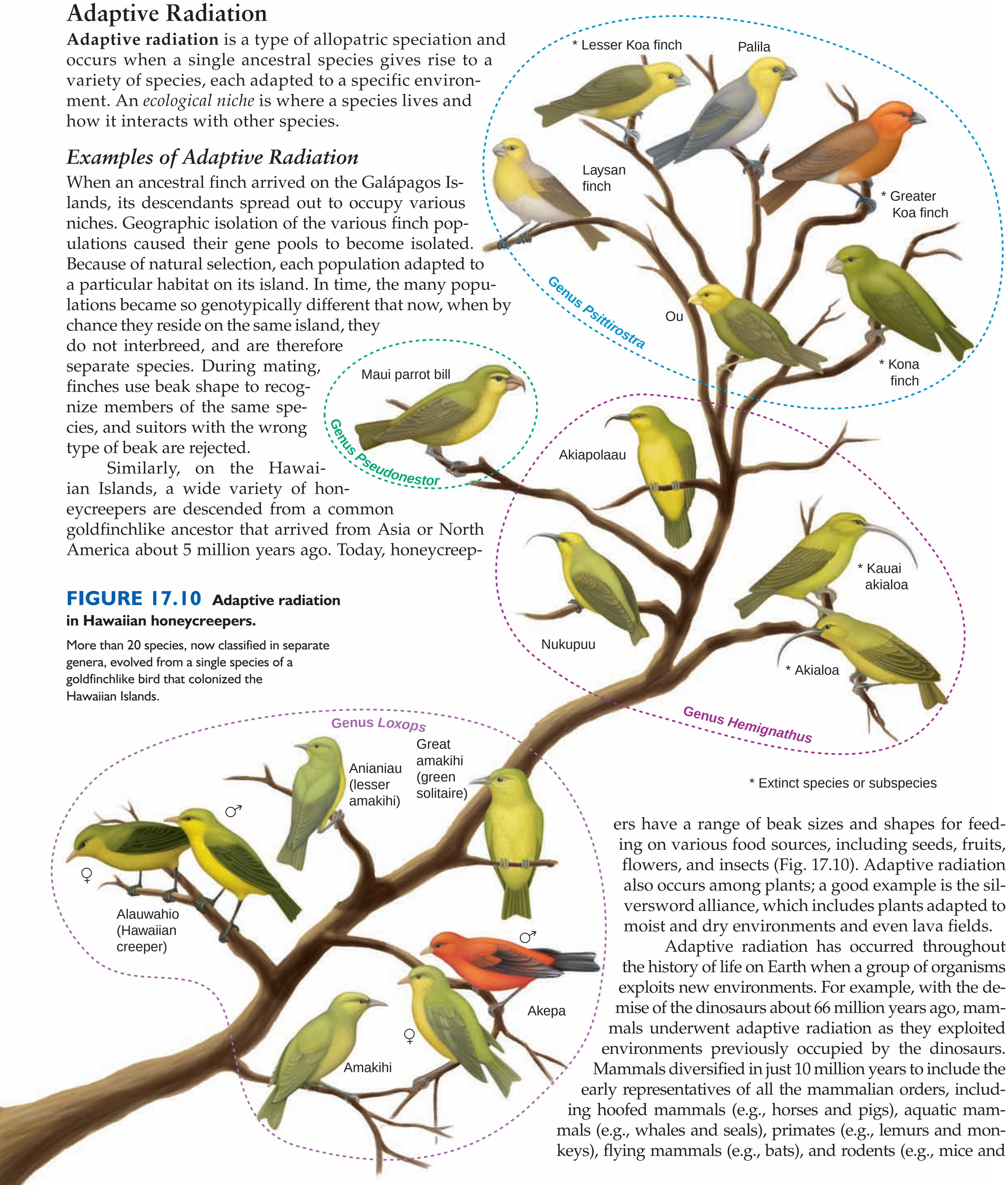


FIGURE 17.10 Adaptive radiation in Hawaiian honeycreepers.

More than 20 species, now classified in separate genera, evolved from a single species of a goldfinchlike bird that colonized the Hawaiian Islands.