

Adaptation and Natural Selection



A tenebrionid beetle (*Stenocara* spp.) perched on a sand dune in the Namib Desert of southwestern Africa. (Insert) Magnified view of the beetle's back shows fog droplets on the wing case (elytra).

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THE NAMIB DESERT, stretching for 1200 miles along the southwest coast of Africa, is home to the highest sand dunes in the world. Rainfall is a rare event in the Namib. But each morning as the Sun rises, the cool, moist air of this coastal desert begins to warm, and the Namib becomes shrouded in fog. Here each morning, black thumbnail-sized beetles perform one of nature's more bizarre behaviors (see photos on chapter opener page). These tenebrionid beetles (*Stenocara* spp.) upend their bodies into a handstand. A beetle stays in this position as fog droplets collect on its back and then gradually roll down the wing case (called the *elytra*) into its mouth. By viewing the bumps on its back through an electron microscope, we can see a wax-coated carpet of tiny nodules covering the sides of the bumps as well as the valleys between them that aid in channeling water from the beetle's back to its mouth.

The tenebrionid beetles of the Namib Desert illustrate two important concepts: the relationship between structure and function, and how that relationship reflects adaptations of the organism to its environment. The structure of the beetle's back and the beetle's behavior of standing on its head in the morning fog serve the function of acquiring water, a scarce and essential resource in this arid environment. These characteristics represent adaptations to life in the unique environment of the Namib Desert. This same set of characteristics, however, are unlikely to be efficient for acquiring water in the desert regions of the continental interior, where morning fog may not form, or in wet environments, such as a tropical rain forest, where standing pools of water are readily available. Each environment presents a different set of constraints on processes relating to survival, growth, and reproduction. The set of characteristics that enable an organism to succeed in one environment typically preclude it from doing equally well under a different set of environmental conditions.

Prior to the mid-19th century this apparent match between species and their environment was seen as the work of the creator. As the late evolutionary ecologist Ernst Mayr of Harvard University so poetically wrote, examples such as the tenebrionid beetles of the Namib Desert served to illustrate the “wise laws that brought about the perfect adaptation of all organisms one to another and to their environment.” Adaptation, after all, implied design—and design, a designer. Natural history was the task of cataloging the creations of the divine architect. By the mid-1800s, however, a revolutionary idea emerged that would forever change our view of nature.

In considering the origin of species, it is quite conceivable that a naturalist . . . might come to the conclusion that species had not been independently created, but had descended, like varieties, from other species. Nevertheless, such a conclusion, even if well founded, would be unsatisfactory, until it could be shown how the innumerable species, inhabiting this world, have been modified, so as to acquire that perfection of structure and coadaptation which justly excites our admiration.

The pages that followed in Charles Darwin's *The Origin of Species*, first published on November 24, 1859, altered the history of science and brought into question a view of the world

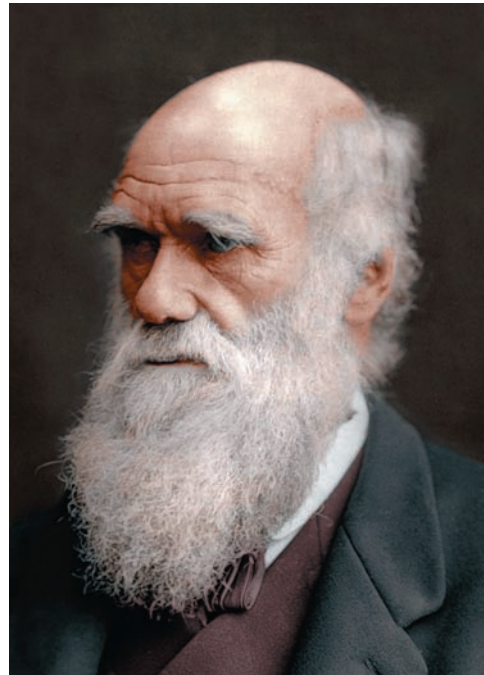


Figure 5.1 Charles Darwin (1809–1882).

that had been held for millennia (**Figure 5.1**). Darwin put forward in those pages a mechanism to explain how the diversity of organisms inhabiting our world have acquired the features seemingly designed to enable them to survive and reproduce. He called it the *theory of natural selection*. Its beauty lay in its simplicity: the mechanism of natural selection is the simple elimination of “inferior” individuals.

5.1 Adaptations Are a Product of Natural Selection

Stated more precisely, **natural selection** is the differential success (survival and reproduction) of individuals within the population that results from their interaction with their environment. As outlined by Darwin, natural selection is a product of two conditions: (1) that variation occurs among individuals within a population in some “heritable” characteristic, and (2) that this variation results in differences among individuals in their survival and reproduction as a result of their interaction with the environment. Natural selection is a numbers game. Darwin wrote:

Among those individuals that do reproduce, some will leave more offspring than others. These individuals are considered more fit than the others because they contribute the most to the next generation. Organisms that leave few or no offspring contribute little or nothing to the succeeding generations and so are considered less fit.

The **fitness** of an individual is measured by the proportionate contribution it makes to future generations. Under a given set of environmental conditions, individuals having certain characteristics that enable them to survive and reproduce are selected

for, eventually passing those characteristics on to the next generation. Individuals without those traits are selected against, failing to pass their characteristics on to future generations. In this way, the process of natural selection results in changes in the properties of populations of organisms over the course of generations, by a process known as **evolution**.

An **adaptation** is any heritable behavioral, morphological, or physiological trait of an organism that has evolved over a period of time by the process of natural selection such that it maintains or increases the fitness (long-term reproductive success) of an organism under a given set of environmental conditions. The concept of adaptation by natural selection is central to the science of ecology. The study of the relationship between organisms and their environment is the study of adaptations. Adaptations represent the characteristics (traits) that enable an organism to survive, grow, and reproduce under the prevailing environmental conditions. Adaptations likewise govern the interaction of the organism with other organisms, both of the same and different species. How adaptations enable an organism to function in the prevailing environment—and conversely, how those same adaptations limit its ability to successfully function in other environments—is the key to understanding the distribution and abundance of species, the ultimate objective of the science of ecology.

5.2 Genes Are the Units of Inheritance

By definition, adaptations are traits that are inherited—passed from parent to offspring. So to understand the evolution of adaptations, we must first understand the basis of inheritance: how characteristics are passed from parent to offspring and what forces bring about changes in those same characteristics through time (from generation to generation).

At the root of all similarities and differences among organisms is the information contained within the molecules of DNA (deoxyribonucleic acid). You will recall from basic biology that DNA is organized into discrete subunits—genes—that form the informational units of the DNA molecule. A **gene** is a stretch of DNA coding for a functional product (ribonucleic acid: RNA). The product is usually messenger RNA (mRNA) and mRNA ultimately results in the synthesis of a protein. The alternate forms of a gene are called **alleles** (derived from the term *allelomorphs*, which in Greek means “different form”).

The process is called gene expression in which DNA is used in the synthesis of products such as proteins. All of the DNA in a cell is collectively called the **genome**.

Genes are arranged in linear order along microscopic, threadlike bodies called **chromosomes**. The position occupied by a gene on the chromosome is called the **locus** (Latin for *place*). In most multicellular organisms, each individual cell contains two copies of each type of chromosome (termed *homologous chromosomes*). In the process of asexual reproduction, both chromosomes are inherited from the single parent. In sexual reproduction, one is inherited from its mother through the ovum and one inherited from its father through the sperm. At any locus, therefore, every diploid individual contains two copies of the gene—one at each corresponding position in the homologous chromosomes. These two copies are the alleles of the gene in that individual. If the two copies of the gene are the same, then the individual is **homozygous** at that given locus. If the two alleles at the locus are different, then the individual is **heterozygous** at the locus. The pair of alleles present at a given locus defines the **genotype** of an individual; therefore, homozygous and heterozygous are the two main categories of genotypes.

5.3 The Phenotype Is the Physical Expression of the Genotype

The outward appearance of an organism for a given characteristic is its **phenotype**. The phenotype is the external, observable expression of the genotype. When an individual is heterozygous, the two different alleles may produce an individual with intermediate characteristics or one allele may mask the expression of the other (**Figure 5.2**). In the case in which one allele masks the expression of the other, the allele that is expressed is referred to as the **dominant allele**, whereas the allele that is masked is called the **recessive allele**. If the allele is recessive, it will only be expressed if the individual is homozygous for that allele (homozygous recessive). If the physical expression of the heterozygous individual is intermediate between those of the homozygotes, the alleles are said to be **incomplete dominance**, and each allele has a specific value (proportional effect) that it contributes to the phenotype.

Phenotypic characteristics that fall into a limited number of discrete categories, such as the example of flower color presented in Figure 5.2, are referred to as **qualitative traits**. Even though all genetic variation is discrete (in the form of alleles),

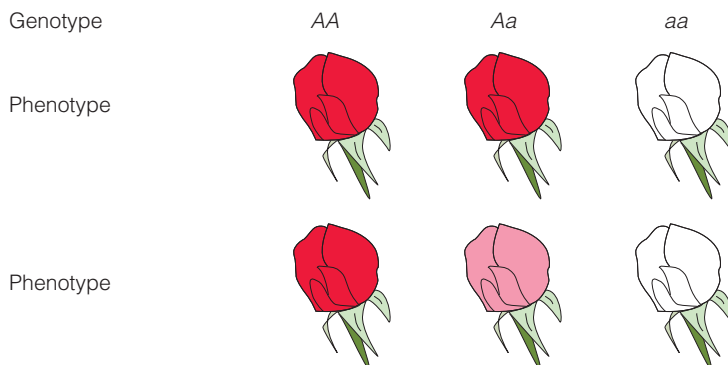


Figure 5.2 Example of different modes of gene expression. In this example, flower color is controlled by a single locus having two alternate alleles, A and a. The A allele codes for the production of red pigment, whereas the a allele does not (absence of pigment). In the first case, heterozygous AA individuals exhibit the same phenotype as homozygous Aa individuals, indicating that A is the dominant allele. The recessive allele (a) is expressed only in homozygous recessive (aa) individuals. In the second case, the heterozygous individuals are intermediate in form to the homozygotes. This is an example of incomplete dominance, and each allele has a proportional effect on the phenotype.

Genotype	# of alleles for red pigment	Phenotype (flower color)
<i>AABB</i>	4	
<i>AABb</i>	3	
<i>AaBB</i>	3	
<i>AAbb</i>	2	
<i>AaBb</i>	2	
<i>aaBB</i>	2	
<i>Aabb</i>	1	
<i>aaBb</i>	1	
<i>aabb</i>	0	

Figure 5.3 Example of phenotypic characteristics controlled by two loci. Assume that flower color is controlled by two genes, each having two alleles (*A*:*a* and *B*:*b*). Both the *A* and *B* alleles code for the production of red pigment, whereas the *a* and *b* alleles do not. There are nine possible genotypes, with the number of alleles coding for red pigment ranging from 4 (*AABB*) to 0 (*aabb*). The resulting phenotypes fall into five categories ranging from dark red through white depending on the number of alleles producing red pigment. The intermediate color (two alleles for red pigment) is the most abundant class. The number of possible phenotypes will increase as the number of loci (genes) controlling the phenotype increases.

most phenotypic traits have a continuous distribution. These traits, such as height or weight, are referred to as **quantitative traits**. The continuous distribution of most phenotypic traits occurs for two reasons. First, most traits have more than one gene locus affecting them. For example, if the phenotypic characteristic of flower color illustrated in Figure 5.2 is controlled by two loci rather than a single locus (each with two alleles—*A*:*a* and *B*:*b*), there are nine possible genotypes (Figure 5.3). In contrast to the three distinct flower colors (phenotypes) produced in the case of a single locus, there is now a range of flower colors varying in hue between dark red and white depending on the number of alleles coding for the production of red pigment (see Figure 5.2). The greater the number of loci, the greater is the range of possible phenotypes. The second factor influencing phenotypic variation is the environment.

5.4 The Expression of Most Phenotypic Traits Is Affected by the Environment

The expression of most phenotypic traits is influenced by the environment; that is to say, the phenotypic expression of the genotype is influenced by the environment. Because environmental factors themselves usually vary continuously—temperature, rainfall, sunlight, level of predation, and so

on—the environment can cause the phenotype produced by a given genotype to vary continuously. To illustrate this point, we can use the example of flower color controlled by two loci presented previously (and in Figure 5.3). Pigment production during flower development can be affected by temperature. If temperatures below some optimal value or range function to reduce the expression of the *A* and *B* alleles in the production of red pigment, fluctuations in temperatures over the period of flower development in the population of plants will function to further increase the range of flower colors (shades between red and white) produced by the nine genotypes.

The ability of a genotype to give rise to different phenotypic expressions under different environmental conditions is termed **phenotypic plasticity**. The set of phenotypes expressed by a single genotype across a range of environmental conditions is referred to as the **norm of reaction** (Figure 5.4). Note that we are not talking about different genotypes adapted to different environmental conditions, but about a single genotype (set

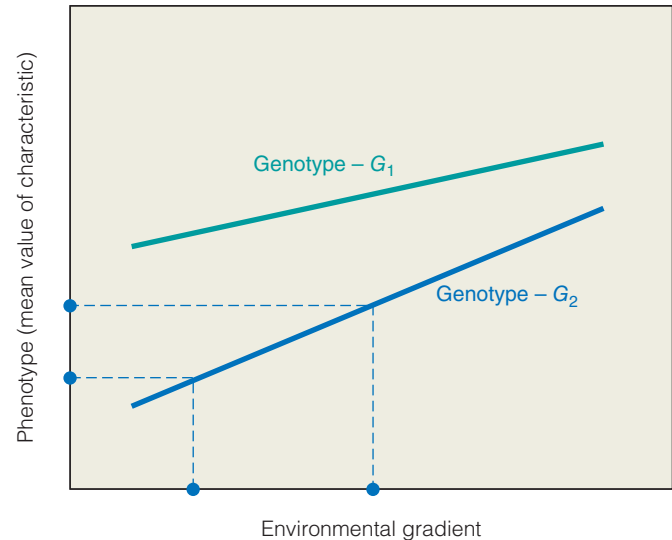


Figure 5.4 A hypothetical example of the norm of reaction: the range of phenotypes expressed by a given genotype in different environments. The norms of reaction for two genotypes, G_1 and G_2 , along an environmental gradient are shown. The two lines represent the mean phenotypic characteristics (such as flower or body coloration) exhibited by two genotypes (G_1 and G_2) at any point along the environmental gradient (such as temperature). The dashed lines illustrate the change in phenotype for G_2 at two different points along the environmental gradient. The ability of a genotype to express different phenotypic characteristics under different environmental conditions is called *phenotypic plasticity*.

Interpreting Ecological Data

- Q1.** Which of the two genotypes (G_1 or G_2) exhibits the greater norm of reaction?
- Q2.** What would the line look like for a genotype that did not exhibit phenotypic plasticity?
- Q3.** Is there any environment in which the two genotypes will express the same phenotype?
- Q4.** Is it possible for the two genotypes to exhibit the same phenotype?

of alleles) capable of altering the development or expression of a phenotypic trait in response to the conditions encountered by the individual organism. The result is the improvement of the individual's ability to survive, grow, and reproduce under the prevailing environmental conditions (i.e., increase fitness). For example, the bodies of many species of insects change in color in response to the prevailing temperature during development (Figure 5.5). Development under colder temperatures typically results in darker coloration. Darker coloration most likely facilitates increased absorption of solar radiation, allowing them to compensate for the lower temperature (see Chapter 7 for discussion of thermoregulation in animals).

Some of the best examples of phenotypic plasticity occur among plants. The size of the plant, the ratio of reproductive tissue to vegetative tissue, and even the shape of the leaves may vary widely at different levels of nutrition, light, moisture, and temperature. An excellent illustration of phenotypic plasticity in plants is the work of Sonia Sultan of Wesleyan University. Sultan's research focuses on phenotypic plasticity in plant species in response to resource availability. In a series of greenhouse experiments, she examined the developmental response of the herbaceous annual *Polygonum lapathifolium* (common name curlytop knotweed) to different light environments. Sultan grew different individuals of the same genotype for eight weeks at two light levels: low light (20 percent available photosynthetically active radiation [PAR]) and high light (100 percent available PAR). Individuals of the same genotype grown under

low-light conditions produced less biomass (slower growth rate), but produced far more photosynthetic leaf area per unit of biomass through changes in biomass allocation, morphology, and structure (Figure 5.6). Individuals grown under low-light conditions produced large, thin leaves and few branches. In contrast, the larger high-light plants grew narrow leaves on many more branches. This response is referred to as **developmental plasticity**. As such, these changes are irreversible. After the adult plant develops, these patterns of biomass allocation (proportions of leaf, stem, and root) will remain largely unchanged, regardless of any changes in the light environment.

In contrast to developmental plasticity, other forms of phenotypic plasticity in response to prevailing environmental



(a)

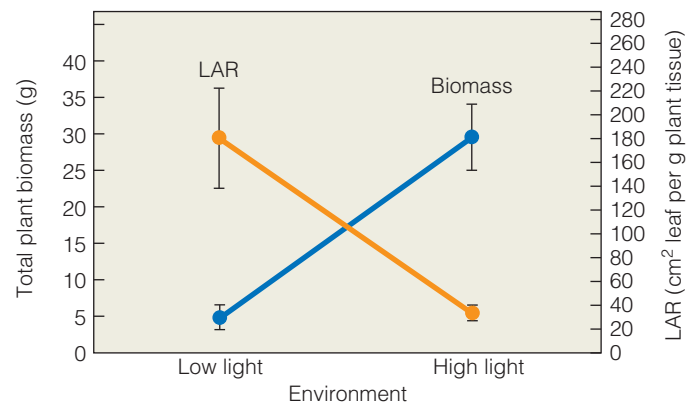


(b)

Figure 5.5 Examples of phenotypic plasticity in insects. The color of many insect species' bodies change in response to temperature during development. (a) Changes in body color in the lubber grasshopper (*Romalea microptera*) from south Florida reared at 35°C (top) and 25°C (bottom). (b) Changes in body color in harlequin bugs (*Murgantia histrionica*). Black individuals were reared at 22°C and yellow individuals at 30°C. (From Whitman and Agrawal 2009.)



(a)



(b)

Figure 5.6 (a) Individuals of the same *Polygonum lapathifolium* genotype grown for eight weeks under low light (20 percent available PAR; left) and high light (100 percent available PAR; right). Low-light plants have large, thin leaves and few branches. The larger high-light grown plant has narrow leaves on many more branches and is more mature (developmentally). (b) Mean norms of reaction for 25 genotypes grown at low light (20 percent PAR) and high light (100 percent PAR). Plants grown under low light have less total biomass, but they produce far more photosynthetic leaf area per unit of total plant biomass (leaf area ratio: LAR) through changes in biomass allocation and leaf morphology. (b) Based on Sultan, S.E. 2000. *Phenotypic plasticity for plant development, function and life history*. Trends in Plant Science 5: 537–542. Figure 2, pg. 538.)

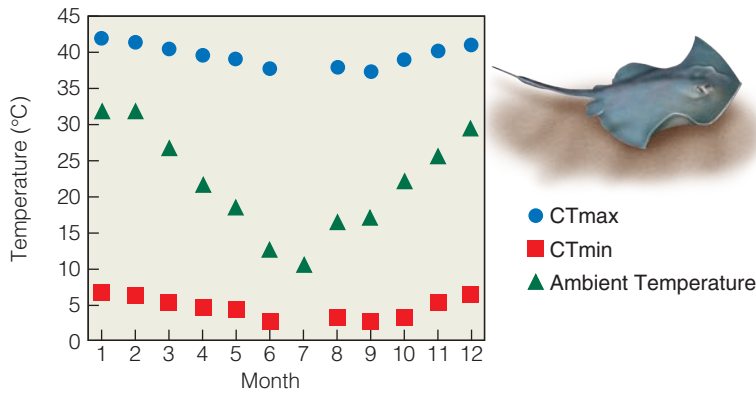


Figure 5.7 Example of seasonal acclimation to ambient temperatures. Plot of mean monthly ambient temperatures and corresponding monthly thermal maximum (T_{max}) and minimum (T_{min}), both in °C, for Atlantic stingray inhabiting St. John’s Bay Florida. (Data from Fangue and Bennett 2003.)

conditions are reversible. For example, fish have an upper and lower limit of tolerance to temperature (see Chapter 7). They cannot survive at water temperatures above and below these limits. However, these upper and lower limits change seasonally as water temperatures warm and cool. This pattern of seasonal change in temperature tolerance is illustrated in the work of Nann Fangue and Wayne Bennett of the University of West Florida. Fangue and Bennett measured seasonal changes in the temperature tolerances of Atlantic stingrays (*Dasyatis sabina*) that inhabit shallow bays of the Florida coast. Their data for individuals inhabiting St. Josephs Bay on the Gulf Coast of Florida show a systematic shift in the critical minimum and maximum temperatures with seasonal changes in the ambient environmental (water) temperature (Figure 5.7). As water temperatures change seasonally, shifts in enzyme and membrane structure allow the individual’s physiology to adjust slowly over a period of time, influencing heart rate, metabolic rate, neural activity, and enzyme reaction rates. These reversible phenotypic changes in an individual organism in response to changing environmental conditions are referred to as **acclimation**.

Acclimation is a common response in both plant and animal species involving adjustments relating to biochemical, physiological, morphological, and behavioral traits.

5.5 Genetic Variation Occurs at the Level of the Population

Adaptations are the characteristics of individual organisms—a reflection of the interaction of the genes and the environment. They are the product of natural selection. Although the process of natural selection is driven by the success or failure of individuals, the population—the collective of individuals and their alleles—changes through time, as individuals either succeed or fail to pass their genes to successive generations. For this reason, to understand the process of adaptation through natural selection, we must first understand how genetic variation is organized within the population.

A species is rarely represented by a single, continuous interbreeding population. Instead, the population of a species is typically composed of a group of subpopulations—local populations of interbreeding individuals, linked to each other in varying degrees by the movement of individuals (see Sections 8.2 and 19.7 for discussion of metapopulations). Thus, genetic variation can occur at two hierarchical levels, within subpopulations and among subpopulations. When genetic variation occurs among subpopulations of the same species, it is called **genetic differentiation**.

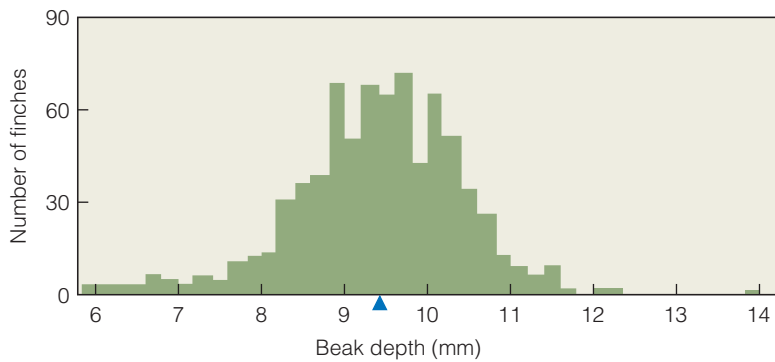


Figure 5.8 Variation in beak size (as measured by depth) in the population of Galápagos medium ground finch (*Geospiza fortis*) on the island of Daphne Major as estimated by individual birds sampled during 1976. The histogram represents the number of individuals that were sampled (y-axis) in each category (0.2 mm) of beak depth (x-axis). The estimate of the population mean is marked by the blue triangle. (Adapted from Grant 1999 after Boag and Grant 1984.)

Interpreting Ecological Data

- Q1.** What type of data do the original measures of beak depth represent? (See Chapter 1, Quantifying Ecology 1.1.)
- Q2.** How have the original measurements of beak depth been transformed for presentation purposes in Figure 5.8?
- Q3.** What is the range (maximum – minimum values) of beak depths observed for the sample of individuals presented in Figure 5.8? (Categories are in units of 0.2 mm.)

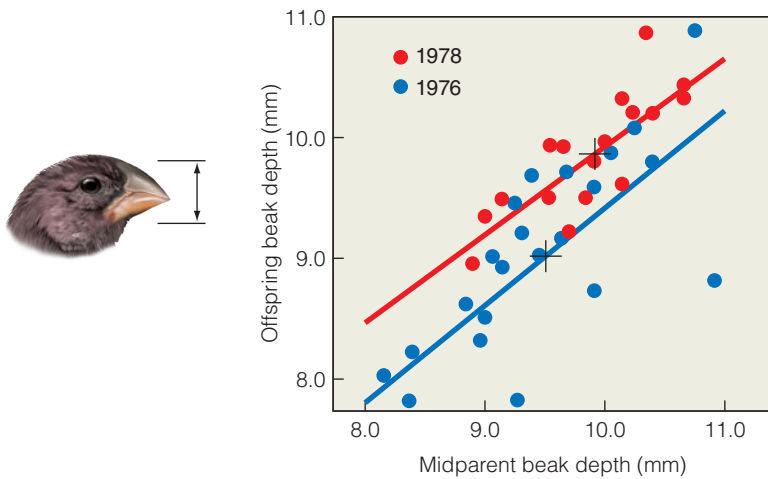


Figure 5.9 The relationship between the beak depth (size) of offspring and their parents in the medium ground finch (*Geospiza fortis*) population on Daphne Major. The x-axis represents midparent beak depth, which is the average beak depth for the two parent birds. The y-axis is the average beak depth of their offspring. The slope of the relationship (represented by the lines) is the estimate of heritability. The blue line and circles are data from 1976, and the red line and circles are data from 1978 (+ signs represent the average values). The results from the two years are consistent (nearly identical slopes); however, the average size of offspring was greater in 1978. Data from both years show a strong relationship between the beak depth of parents and their offspring. (Adapted from Grant 1999 after Boag 1983.)

The sum of genetic information (alleles) across all individuals in the population is referred to as the **gene pool**. The gene pool represents the total genetic variation within a population. Genetic variation within a population can be quantified in several ways. The most fundamental measures are **allele frequency** and **genotype frequency**. The word *frequency* in this context refers to the proportion of a given allele or genotype among all the alleles or genotypes present at the locus in the population.

5.6 Adaptation Is a Product of Evolution by Natural Selection

We have defined evolution as changes in the properties of populations of organisms over the course of generations (Section 5.1). More specifically, phenotypic evolution can be defined as a change in the mean or variance of a phenotypic trait across generations as a result of changes in allele frequencies. In favoring one phenotype over another, the process of natural selection acts directly on the phenotype. But in doing so, natural selection changes allele frequencies within the population. Changes in allele frequencies from parental to offspring generations are a product of differences in relative fitness (survival and reproduction) of individuals in the parental generation.

The work of Peter Grant and Rosemary Grant provides an excellent documented example of natural selection. The Grants have spent more than three decades studying the birds of the Galápagos Islands, the same islands whose diverse array of animals so influenced the young Darwin when he was a naturalist aboard the expeditionary ship HMS *Beagle*. Among other events, the Grants' research documented a dramatic shift in a physical characteristic of finches inhabiting some of these islands during a period of extreme climate change.

Recall from our initial discussion in Section 5.1 that natural selection is a product of two conditions: (1) that variation occurs among individuals within a population in some heritable characteristic and (2) that this variation results in differences among individuals in their survival and reproduction. **Figure 5.8** shows variation in beak size in Darwin's

medium ground finch (*Geospiza fortis*) on the 40-hectare islet of Daphne Major, one of the Galápagos Islands off the coast of Ecuador. Heritability of beak size in this species was established by examining the relationship between the beak size of parents and their offspring (**Figure 5.9**).

Beak size is a trait that influences the feeding behavior of these seed-eating birds. Individuals with large beaks can feed on a wide range of seeds, from small to large, whereas individuals with smaller beaks are limited to feeding on smaller seeds (**Figure 5.10**).

During the early 1970s, the island received an average rainfall of between 127 and 137 millimeters (mm) per year, supporting an abundance of seeds and a large finch population

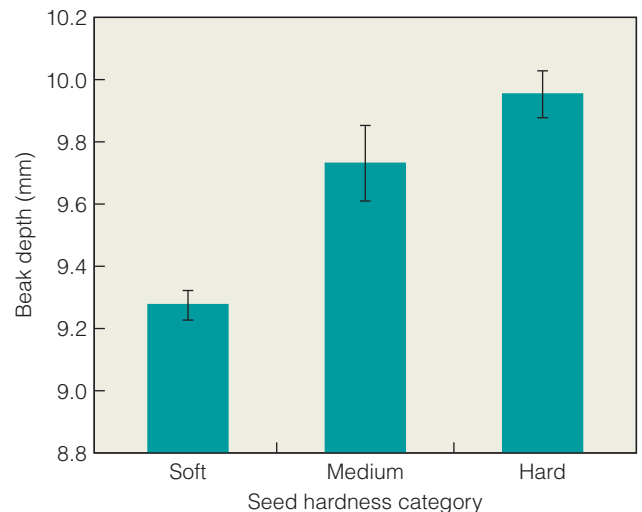


Figure 5.10 Beak depth of medium ground finches (*Geospiza fortis*) feeding on soft, medium, and hard seeds on Daphne Major in 1977. The bars represent the mean beak depth for birds feeding on the corresponding class of seeds, and the lines represent ± 1 standard error. As can be seen, beak size has a direct influence on the hardness and size of seeds selected by individual birds. (After Boag and Grant 1984.)

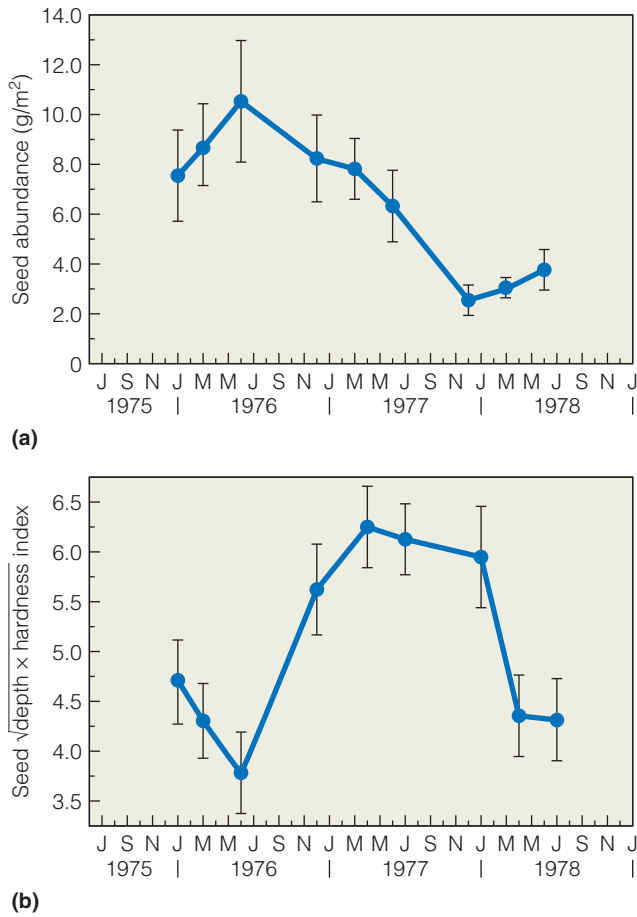


Figure 5.11 Changes in (a) seed abundance and (b) seed size and hardness on Daphne Major for the period of July 1975 to July 1978. Points represent mean values, and associated lines represent the 95 percent confidence intervals. Seed size and hardness index is the square root of the product of seed depth and hardness.
(Adapted from Grant 1999 after Boag and Grant 1981.)

(1500 birds). In 1977, however, a periodic shift in the climate of the eastern Pacific Ocean—called La Niña—altered weather patterns over the Galápagos, causing a severe drought (see Chapter 2, Section 2.9). That season, only 24 mm of rain fell. During the drought, seed production declined drastically. Small seeds declined in abundance faster than large seeds did, increasing the average size and hardness of seeds available (Figure 5.11). The decline in food (seed) resources resulted in an 85 percent decline in the finch population as a result of mortality and possible emigration (Figure 5.12a). Mortality, however, was not equally distributed across the population (Figure 5.12b). Small birds had difficulty finding food, whereas large birds, especially males with large beaks, had the highest rate of survival because they were able to crack large, hard seeds.

The graph in Figure 5.12b represents a direct measure of the differences in fitness (as measured by survival) among individuals in the population as a function of differences in phenotypic characteristics (beak size), the second condition for

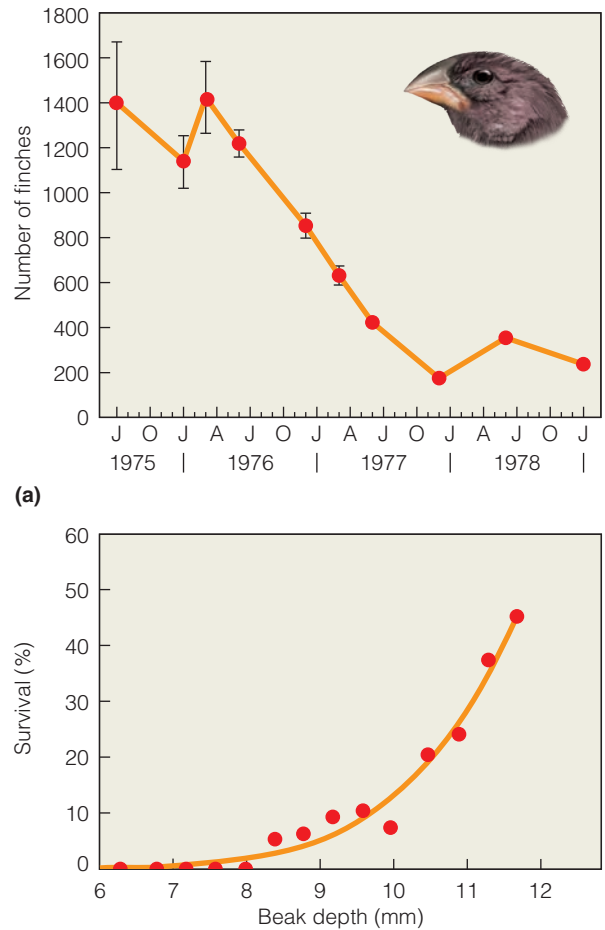


Figure 5.12 (a) Decline of the population of the medium ground finch on Daphne Major during the 1977 drought. Points represent mean estimates, and associated lines represent the 95 percent confidence interval. The population declined in the face of seed scarcity during a prolonged drought (Figure 5.11a). (b) Birds with larger beak size had a much greater rate of survival as a result of their ability to feed on the larger, harder seeds that comprised the majority of food resources during the drought period (see Figure 5.11b).
(Adapted from Grant 1999 after Boag and Grant 1981.)

natural selection. The phenotypic trait that selection acts directly upon is referred to as the **target of selection**; in this example, it is beak size. The **selective agent** is the environmental cause of fitness differences among organisms with different phenotypes, or in this case, the change in food resources (abundance and size distribution of seeds).

The increased survival rate of individuals with larger beaks resulted in a shift in the distribution of beak size (phenotypes) in the population (Figure 5.13). This type of natural selection, in which the mean value of the trait is shifted toward one extreme over another (Figure 5.14a), is called **directional selection**. In other cases, natural selection may favor individuals near the population mean at the expense of the two extremes; this is referred to as **stabilizing selection** (Figure 5.14b). When natural selection favors both extremes simultaneously,

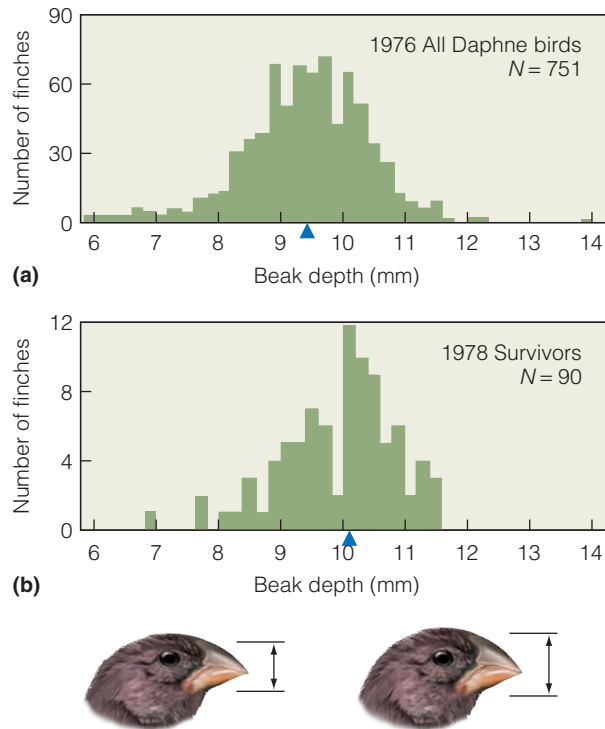


Figure 5.13 Distribution of beak depth for the population of medium ground finches inhabiting Daphne Major (a) before and (b) after natural selection. The estimate of mean beak depth for both census periods is shown by the blue triangles. Note the increase in the mean beak depth for the population resulting from the differential survival of individuals related to beak size as shown in Figure 5.12.

(Adapted from Grant 1999 after Boag and Grant 1984.)

although not necessarily to the same degree, it can result in a bimodal distribution of the characteristic(s) in the population (**Figure 5.14c**). Such selection, known as **disruptive selection**, occurs when members of a population are subject to different selection pressures.

The work of Beren Robinson of Guelph University in Canada provides an excellent example of disruptive selection. In studying the species of threespine stickleback (*Gasterosteus aculeatus*), which occupies Cranby Lake in the coastal region of British Columbia, Robinson found that individuals sampled from the open-water habitat (limnetic habitat) differed morphologically from individuals sampled from the shallower nearshore waters (benthic habitat). In a series of experiments, Robinson established that these individuals represented distinct phenotypes that are products of natural selection promoting divergence within the population. He initially established that morphological differences between the two forms were heritable, rather than an expression of phenotypic plasticity in response to the two different habitats or diets. He reared offspring of the two forms under identical laboratory conditions (environmental conditions and diet) and although there was some degree of phenotypic plasticity, differences in most characteristics remained between the two forms. On average, the benthic form (BF) had

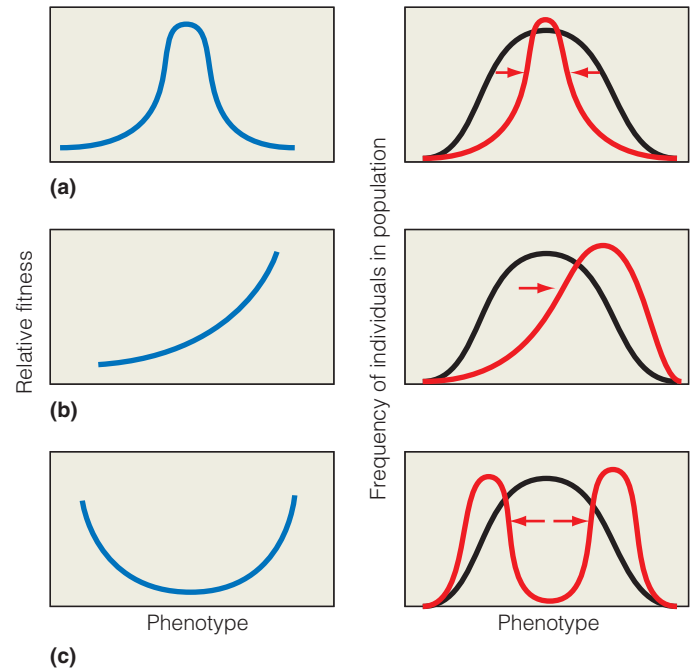


Figure 5.14 Three types of selection: curves in the left column represent the relative fitness of different phenotypes in the population under the three types of selection, whereas curves in the right column show the changes in the frequency of individuals in the population exhibiting different phenotypes under the corresponding three types of selection. Arrows represent the direction of change in the distribution of phenotypes in the population. (a) Under stabilizing selection, the mean phenotype in the population exhibits the highest relative fitness and the original distribution of phenotypes (black curve) is shifted to the center (mean value). (b) In directional selection, the distribution of phenotypes is shifted to one extreme. (c) In disruptive selection, the relative fitness is greatest for the extreme values of phenotype and the result is a bimodal distribution of phenotypes in the population.

Interpreting Ecological Data

Q1. Figure 5.12b shows the survival of ground finches as a function of beak size during the period of drought. How does the graph in Figure 5.12b relate to this figure?

Q2. How do the patterns of relative fitness shown in the graphs on the left-hand column give rise to the corresponding patterns of selection illustrated by the arrows in the graphs shown in the right-hand column?

(1) shorter overall body length, (2) deeper body, (3) wider mouth, (4) more dorsal spines, and (5) fewer gill rakers than did the limnetic form (LF) (**Figure 5.15a**).

The two habitats in the lake—benthic and limnetic—provide different food resources; so to determine the agent of selection that caused divergence within the population, Robinson conducted feeding trials in the laboratory to test for trade-offs in the foraging efficiency of the two forms on food resources found in the two habitats. The foraging success of individual fish was assessed in two artificial habitats, mimicking conditions in the limnetic and benthic environments.

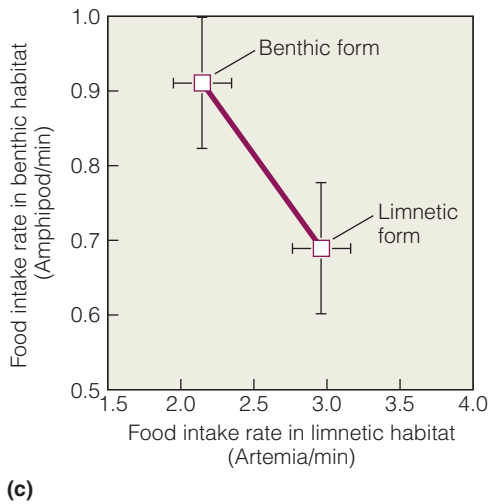
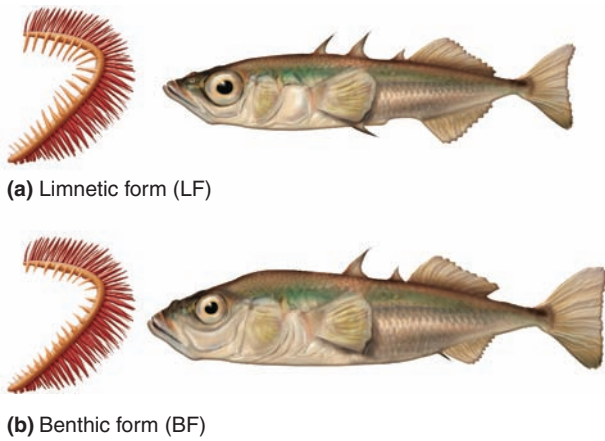


Figure 5.15 Morphological differences in the gill rakers of the stickleback species based on (a) limnetic form (phenotype) and (b) benthic form (phenotype) feeding habits. (c) Mean intake rate (and standard errors) of limnetic (open) and benthic (shallow) forms in open-water (food source: *Artemia* [brine shrimp larvae]) and shallow-water, benthic (food source: amphipod) feeding trials. [(a) Illustration by Laura Nagel, Queen's University. From Schuller 1993; (b) Adapted from Robinson 2000.]

Two food types were used in the trials. Brine shrimp larvae (*Artemia*), a common prey found in open water, were placed in the artificial limnetic habitats. Larger amphipods, fast-moving arthropods with hard exoskeletons that forage on dead organic matter on the sediment surface, were placed in the artificial benthic habitats.

Results of the foraging trials revealed distinct differences in the foraging success of the two morphological forms (phenotypes; **Figure 5.15b**). The LF individuals were most successful at foraging on the brine shrimp larvae. They had a higher consumption rate and required only half the number of bites to consume as compared to the BF individuals. In contrast, BF individuals had a higher intake rate for amphipods and on average consumed larger amphipods than did LF individuals.

Robinson was able to determine that the higher intake rate of brine shrimp larvae by LF individuals was related to this form's greater number of gill rakers, and greater mouth width was related to the higher intake rate of amphipods by BF individuals. Therefore, he found that foraging efficiency was related to morphological differences between the two forms, suggesting that divergent selection in the two distinct phenotypes represents a trade-off in characteristics related to the successful exploitation of these two distinct habitats and associated food resources.

5.7 Several Processes Other than Natural Selection Can Function to Alter Patterns of Genetic Variation within Populations

Natural selection is the only process that leads to adaptation because it is the only one in which the changes in allele frequency from one generation to the next are a product of differences in the relative fitness (survival and reproduction) of individuals in the population. Yet not all phenotypic characteristics represent adaptations, and processes other than natural selection can be important factors influencing changes in genetic variation (allele and genotype frequencies) within populations. For example, mutation is the ultimate source of the genetic variation that natural selection acts upon. **Mutations** are heritable changes in a gene or a chromosome. The word *mutation* refers to the process of altering a gene or chromosome as well as to the product, the altered state of the gene or chromosome. Mutation is a random force in evolution that produces genetic variation. Any altered phenotypic characteristic resulting from mutation may be beneficial, neutral, or harmful. Whether a mutation is beneficial depends on the environment. A mutation that enhances an organism's fitness in one environment could harm it in another. Most of the mutations that have significant effect, however, are harmful, but the harmful mutations do not survive long. Natural selection eliminates most deleterious genes from the gene pool, leaving behind only genes that enhance (or at least do not harm) an organism's ability to survive, grow, and reproduce in its environment.

Another factor that can directly influence patterns of genetic variation within a population is a change in allele frequencies as a result of random chance—a process known as **genetic drift**. Recall from basic biology that the recombination of alleles in sexual reproduction is a random process. The offspring produced in sexual reproduction, however, represent only a subset of the parents' alleles. If the parents have only a small number of offspring, then not all of the parents' alleles will be passed on to their progeny as a result of the random assortment of chromosomes at meiosis (the process of recombination). In effect, genetic drift is the evolutionary equivalent of sampling error, with each successive generation representing only a subset or sample of the gene pool from the previous generation.

In a large population, genetic drift will not affect each generation much because the effects of the random nature of

the process will tend to average out. But in a small population, the effect could be rapid and significant. To illustrate this point, we can use the analogy of tossing a coin. With a single toss of the coin, the probability of each of the two possible outcomes, heads or tails, is equal, or 50 percent. Likewise, with a series of four coin tosses, the probability of the outcome being two heads and two tails is 50 percent. But each individual outcome in the coin tosses is independent; therefore, in a series of four coin tosses, there is also a probability of 0.0625, or 6.25 percent, that the outcome will be four heads. The probability of the outcome being all heads drops to 9.765×10^{-4} if the number of tosses is increased to 10, and this probability drops to 8.88×10^{-16} for 50 tosses. Likewise, the probability of heterozygous (*Aa*) individuals in the population producing only homozygous (either *aa* or *AA*) offspring under a system of random mating decreases with increasing population size.

Patterns of genetic variation within a population can also be influenced by the movement of individuals into, or out of, the population. Recall from the discussion of genetic variation in Section 5.5 that the population of a species is typically composed of a group of subpopulations—local populations of interbreeding individuals that are linked to one another in varying degrees by the movement of individuals (see Chapter 8). **Migration** is defined as the movement of individuals between local populations, whereas **gene flow** is the movement of genes between populations (see Chapter 8). Because individuals carry genes, the terms are often used synonymously; however, if an individual immigrates into a population but does not successfully reproduce, the new genes are not established in the population. Migration is a potent force in reducing the level of population differentiation (genetic differences among local populations; see Section 5.5).

One of the most important principles of genetics is that under conditions of random mating, and in the absence of the factors discussed thus far—natural selection, mutation, genetic drift, and migration—the frequency of alleles and genotypes in a population remains constant from generation to generation. In other words, no evolutionary change occurs through the process of sexual reproduction itself. This principle, referred to as the **Hardy–Weinberg principle**, is named for Godfrey Hardy and Wilhelm Weinberg, who each independently published the model in 1908 (see **Quantifying Ecology 5.1**). Mating is random when the chance that an individual mates with another individual of a given genotype is equal to the frequency of that genotype in the population. When individuals choose mates nonrandomly with respect to their genotype—or more specifically, select mates based on some phenotypic trait—the behavior is referred to as **assortative mating**. Perhaps the most recognized and studied form of assortative mating is female mate choice. Female mate choice is the behavior in which females exhibit a bias toward certain males as mates based on specific phenotypic traits (often secondary sex characteristics), such as body size or coloration (see Chapter 10, Section 10.11).

Positive assortative mating occurs when mates are phenotypically more similar to each other than expected by

chance. Positive assortative mating is common, and one of the most widely reported examples relates to the timing of reproduction. Plants mate assortatively based on flowering time. In populations of plants with an extended flowering time, early flowering plants are often no longer flowering when late flowering plants are in bloom.

The genetic effect of positive assortative mating is an increase in the frequency of homozygotes with a decrease in the frequency of heterozygotes in the population. Think of a locus where *AA* individuals tend to be larger than *Aa*, which in turn are larger than *aa* individuals. With positive assortative mating, *AA* will mate with *AA*, and *aa* with other *aa*. All of these matings will produce only homozygous offspring. Even mating between *Aa* individuals will result in half of the offspring being homozygous. The genetic effects of positive assortative mating are only at the loci that affect the phenotypic characteristic by which the organisms are selecting mates.

Negative assortative mating occurs when mates are phenotypically less similar to each other than expected by chance. Though not as common as positive assortative mating, negative assortative mating results in an increase in the frequency of heterozygotes.

A special case of nonrandom mating is inbreeding. **Inbreeding** is the mating of individuals in the population that are more closely related than expected by random chance. Unlike positive assortative mating, inbreeding increases homozygosity at all loci. Inbreeding affects all loci equally because related individuals are genetically similar by common ancestry, and they are therefore more likely to share alleles throughout the genome than unrelated individuals.

Inbreeding can be detrimental. Offspring are more likely to inherit rare, recessive, deleterious genes. These genes can cause decreased fertility, loss of vigor, reduced fitness, reduced pollen and seed fertility in plants, and even death. These consequences are referred to as **inbreeding depression**.

As we have seen from the preceding discussion, nonrandom mating changes genotypic frequencies from one generation to the next, but assortative mating does not directly result in a change of allele frequencies within a population. The other three processes discussed—mutation, migration, and genetic drift, together with natural selection—alter the allele frequencies, and therefore result in a shift in the distribution of genotypes (and potentially phenotypes) within the population. As such, all four processes function as agents of evolution. However, natural selection is special among the four evolutionary processes because it is the only one that leads to adaptation. The other three can only speed up or slow the development of adaptations.

5.8 Natural Selection Can Result in Genetic Differentiation

The example of natural selection in the population of medium ground finches as described previously represents a shift in the distribution of phenotypes in the population inhabiting the island of Daphne Major in response to environmental changes