# Chapter 23

# The Evolution of Populations

**Overview: The Smallest Unit of Evolution**

- One common misconception about evolution is that individual organisms evolve, in a Darwinian sense, during their lifetimes.
  - Natural selection does act on *individuals*. Each individual's traits affect its survival and its reproductive success relative to other individuals in the population.
  - The evolutionary impact of natural selection is apparent only in the changes in a *population* of organisms over time.
  - It is the population, not the individual, which evolves.
- Consider the example of the medium ground finch *(Geospiza fortis)*, a seed-eating bird that lives on the Galápagos Islands.
  - In 1977, the *G. spiza* population endured a long period of drought. Of 1200 birds, only 180 survived.
  - The surviving finches had larger, deeper beaks than the finches that died.
  - Soft, small seeds were in short supply during the drought.
  - Large, hard seeds were more abundant.
  - Finches with large, deep beaks could crack the large seeds and thus were able to survive the food shortage during the drought.
- Following the drought, the average beak size in the population was larger than before the drought. The finch population had evolved larger beaks by natural selection.
  - *Individual* finches did not evolve. Each bird had a beak of a particular size, which did not grow larger during the drought.
  - The proportion of birds with large beaks in the population increased from generation to generation because birds with large beaks were better able to survive the drought and reproduce successfully.
- **Microevolution** is defined as a change in allele frequencies in a population over time.

- Three mechanisms can cause allele frequencies to change: natural selection, genetic drift (chance events that alter allele frequencies), and gene flow (the transfer of alleles between populations).
- Natural selection is the only mechanism of adaptive evolution, improving the match between organisms and their environment.

## Concept 23.1 Genetic variation makes evolution possible

- Charles Darwin proposed that natural selection was the primary mechanism for change in species over time.
  - Darwin recognized that variation in heritable traits was a prerequisite for evolution, but he did not know exactly how organisms pass heritable traits to their offspring.
- Just a few years after Darwin published *The Origin of Species*, Gregor Mendel proposed a model of inheritance that supported Darwin's theory.
  - Mendel's particulate hypothesis of inheritance stated that parents pass on discrete heritable units (genes) that retain their identities in offspring.
  - Although Mendel and Darwin were contemporaries, Darwin never saw Mendel's paper.
  - Mendel's ideas set the stage for an understanding of the genetic differences on which evolution is based.

***Genetic variation occurs within a population.***

- Individual variation occurs in all species and often reflects **genetic variation**, differences among individuals in the composition of their genes or other DNA segments.
- However, not all phenotypic variation is heritable. Phenotype is the product of an inherited genotype and environmental influences.
- Only the genetic component of variation has evolutionary consequences.
- Both quantitative and discrete characters contribute to variation *within* a population.
- *Discrete characters,* such as flower color, are usually determined by a single locus with different alleles that produce distinct phenotypes.
- *Quantitative characters* vary along a continuum within a population.
  - For example, plant height in a wildflower population ranges from short to tall.
  - Quantitative variation is usually due to polygenic inheritance in which the additive effects of two or more genes influence a single phenotypic character.
- Biologists can measure genetic variation in a population at the whole-gene level (*gene variability*) and at the molecular level of DNA (*nucleotide variability*).
- **Average heterozygosity** measures gene variability, the average percent of gene loci that are heterozygous.
  - In the fruit fly *(Drosophila)*, about 86% of their 13,700 gene loci are homozygous (fixed).
  - About 14% (1,920 genes) are heterozygous, for an average heterozygosity of 14%.
  - This level of genetic variation provides ample raw material for natural selection to operate, resulting in evolutionary change.
- Average heterozygosity can be estimated using protein gel electrophoresis, which measures differences in the protein products of genes. This approach does not measure silent mutations that do not alter the amino acid sequence of a protein.
  - PCR-based approaches or restriction fragment analyses do detect silent mutations.
- **Nucleotide variability** measures the mean level of difference in nucleotide sequences (base-pair differences) among individuals in a population.
  - In fruit flies, about 1% of the bases differ between two individuals.
  - Two individuals differ, on average, at 1.8 million of the 180 million nucleotides in the fruit fly genome.

- Average heterozygosity tends to be greater than nucleotide diversity because a gene can consist of thousands of bases of DNA. A difference at only one of these bases is sufficient to make two alleles of that gene different and count toward average heterozygosity.

***Genetic variation occurs between populations.***

- Species also exhibit **geographic variation**, differences in the genetic composition of geographically separate populations.
  - Natural selection contributes to geographic variation by modifying gene frequencies in response to differences in local environmental factors.
  - Genetic drift can also lead to variation among populations through the cumulative effect of random fluctuations in allele frequencies.
- Geographic variation in the form of graded change in a trait along a geographic axis is called a **cline.**
  - Clines may reflect the influence of natural selection based on gradation in some environmental variable.

***New genes and new alleles originate only by mutation.***

- The genetic variation on which evolution depends originates when mutation, gene duplication, or other processes produce new alleles and new genes.
  - The process of sexual reproduction can also result in genetic variation as existing alleles and genes are arranged in new ways.
- New alleles can arise by *mutation*, a change in the nucleotide sequence of an organism's DNA.
- In multicellular organisms, only mutations in cell lines that form gametes can be passed on to offspring.
  - In fungi and plants, many different cell lines can produce gametes.
  - In animals, most mutations occur in somatic cells and are lost when the individual dies.
- A point mutation is a change of a single base in a gene.
- Point mutations can have a significant impact on phenotype, as in the case of sickle-cell disease.
- Most point mutations are harmless.
  - Much of the DNA in eukaryotic genomes does not code for protein products.
  - Because the genetic code is redundant, some point mutations in genes that code for proteins may not alter the protein's amino acid composition.
  - Even if there is a change in an amino acid as a result of a point mutation, it may not affect the protein's shape and function.
- On rare occasions, a mutant allele may actually make its bearer better suited to the environment, increasing its reproductive success.
- Some mutations alter gene number or position.
  - Chromosomal mutations that delete, disrupt, or rearrange many loci at once are usually harmful.
  - In rare cases, chromosomal rearrangements may be beneficial.
    - For example, the translocation of part of one chromosome to a different chromosome could link genes that act together for a positive effect.
- Gene duplication is an important source of new genetic variation.
  - Duplication may occur due to errors in meiosis, slippage during DNA replication, or the activities of transposable elements.
  - Duplications of large chromosome segments are often harmful, but the duplication of small pieces of DNA may not be.

- Duplicated segments can persist over generations and provide new loci that may eventually take on new functions by mutation and subsequent selection.
    - The result is an expanded genome with new genes that may take on new functions.

- Beneficial increases in gene number appear to have played a major role in evolution.
    - For example, mammalian ancestors carried a single gene for detecting odors that has been duplicated many times.
    - Modern humans have about 1,000 olfactory receptor genes and mice have 1,300.
    - Dramatic increases in the number of olfactory genes benefited early mammals, enabling them to detect faint odors and distinguish among smells.
    - Because of mutations, 60% of these genes have been inactivated in humans.
    - Mice, which rely more on their sense of smell, have lost only 20% of their olfactory receptor genes.
    - Since mutation rates in humans and mice are similar, this difference is likely due to strong selection against mice with mutations that affect their olfactory genes
- Some genetic variation in populations represents **neutral variation** that does not confer selective advantage or disadvantage.
- However, variation is also found at loci affected by selection. What prevents natural selection from reducing genetic variation by culling all unfavorable alleles?
- The tendency for natural selection to reduce variation is countered by mechanisms that preserve or restore variation, including diploidy and balanced polymorphisms.
- Diploidy in eukaryotes prevents the elimination of recessive alleles via selection because recessive alleles do not affect the phenotype in heterozygotes.
    - Even recessive alleles that are unfavorable can persist in a population through their propagation by heterozygous individuals.
- Recessive alleles are exposed to selection only when both parents carry the same recessive allele and combine two recessive alleles in one zygote.
    - This happens only rarely when the frequency of the recessive allele is very low.
    - The rarer the recessive allele, the greater the degree of protection it has from natural selection.
- Heterozygote protection maintains a huge pool of alleles that may not be suitable under the present conditions but may become beneficial when the environment changes.
- Natural selection itself preserves variation at some gene loci.

***Mutation rates vary from organism to organism.***

- Rates of mutations that affect phenotype average about $10^{-5}$ mutations per gene per gamete in each generation (in other words, about one mutation for every 100,000 genes) in plants and animals.
    - In microorganisms and viruses with short generation spans, mutations can quickly generate genetic variation within populations.
- For example, HIV has a generation time of two days. It also has an RNA genome, which has a higher mutation rate than a DNA genome because of the lack of RNA repair mechanisms in host cells.
    - As a result, it is unlikely that a single drug treatment will ever be effective against HIV. Mutant forms of the virus that are resistant to the drug will arise and proliferate.

- The most effective treatments are drug “cocktails” because it is unlikely that multiple mutations will confer resistance to *all* of the drugs in the cocktail.

***Sexual reproduction produces unique combinations of alleles.***

- In sexually reproducing populations, most of the genetic variation results from the unique combinations of alleles that each individual receives.
- Variant alleles originated from past mutations. However, sexual reproduction shuffles variant alleles and deals them at random to produce unique individual genotypes.
- Three mechanisms contribute to the shuffling: crossing over, independent assortment of chromosomes, and fertilization.
- The combined effects of these three mechanisms ensure that sexual reproduction rearranges existing alleles into new combinations each generation, providing the genetic variation that makes evolution possible.

## Concept 23.2 The Hardy-Weinberg equation can be used to test whether a population is evolving

- For a population to evolve, individuals must differ genetically *and* one of the factors that causes evolution must be at work.

***A population’s gene pool is defined by its allele frequencies.***

- A **population** is a group of individuals of the same species that live in the same area and interbreed to produce fertile offspring.
- Populations of a species may be isolated from each other and rarely exchange genetic material.
- Members of a population are more likely to breed with members of the same population than with members of other populations.
- The total aggregate of all the alleles for all of the loci for all of the individuals in a population is called the population’s **gene pool**.
  - If only one allele exists at a particular locus in a population, that allele is said to be *fixed* in the gene pool, and all individuals will be homozygous for that gene.
  - If there are two or more alleles at a particular locus, then individuals can be either homozygous or heterozygous for that gene.
- Each allele has a frequency or proportion in the population’s gene pool.
- For example, imagine a population of 500 wildflower plants with two alleles ($C^R$ and $C^W$) at a locus that codes for flower pigment.
  - Suppose that in the imaginary population of 500 plants, 20 (4%) are homozygous for the $C^W$ allele ($C^WC^W$) and have white flowers.
  - Of the remaining plants, 320 (64%) are homozygous for the $C^R$ allele ($C^RC^R$) and have red flowers.
  - These alleles show incomplete dominance, so 160 (32%) of the plants are heterozygous ($C^RC^W$) and produce pink flowers.
- Because these plants are diploid, the population of 500 plants has 1,000 copies of the gene for flower color.
  - The dominant allele ($C^R$) accounts for 800 copies ($320 \times 2$ for $C^RC^R$ + $160 \times 1$ for $C^RC^W$).

- The frequency of the $C^R$ allele in the gene pool of this population is 800/1,000 = 0.8, or 80%.
- The $C^W$ allele must have a frequency of 1.0 − 0.8 = 0.2, or 20%.

- When there are two alleles at a locus, the convention is to use *p* to represent the frequency of one allele and *q* to represent the frequency of the other.
  - Thus *p*, the frequency of the $C^R$ allele in this population, is 0.8.
  - The frequency of the $C^W$ allele, represented by *q*, is 0.2.
- Allele and genotype frequencies can be used to test whether evolution is occurring in a population.

***The Hardy-Weinberg principle describes a non-evolving population.***

- Population geneticists determine what the genetic makeup of a population would be if it were *not* evolving.
- We can then compare data from a real population to what we would expect to see if the population was not evolving.
- If we find differences, we can conclude that the population is evolving, and then try to figure out why.
- The **Hardy-Weinberg principle** describes the gene pool of a population that is not evolving.
- The Hardy-Weinberg principle states that the frequencies of alleles and genotypes in a population's gene pool will remain constant over generations unless acted upon by agents other than Mendelian segregation and recombination of alleles.
  - The shuffling of alleles by meiosis and random fertilization has no effect on the overall gene pool of a population.
  - Such a gene pool is said to be in *Hardy-Weinberg equilibrium*.
- In our imaginary wildflower population of 500 plants, 80% (0.8) of the flower-color alleles are $C^R$ and 20% (0.2) are $C^W$.
- How will meiosis and sexual reproduction affect the frequencies of the two alleles in the next generation?
- Because each gamete has only one allele for flower color, we expect that a gamete drawn from the gene pool at random has a 0.8 chance of bearing a $C^R$ allele and a 0.2 chance of bearing a $C^W$ allele.
- Suppose that the individuals in a population not only donate gametes to the next generation at random but also mate at random. In other words, all male-female matings are equally likely.
  - The allele frequencies in this population will not change from one generation to the next. Its genotype frequencies, which can be predicted from the allele frequencies, will also remain unchanged.
- For the flower-color locus, the population's genetic structure is in a state of Hardy-Weinberg equilibrium.
  - Using the rule of multiplication for probabilities, we can determine the frequencies of the three possible genotypes in the next generation.
  - The probability of picking two $C^R$ alleles (to obtain a $C^RC^R$ genotype) is 0.8 × 0.8 = 0.64, or 64%.
  - The probability of picking two $C^W$ alleles (to obtain a $C^WC^W$ genotype) is 0.2 × 0.2 = 0.04, or 4%.
  - Heterozygous individuals are either $C^RC^W$ or $C^WC^R$, depending on whether the $C^R$ allele arrived via sperm or egg.
  - The probability of being heterozygous (with a $C^RC^W$ genotype) is 0.8 × 0.2 = 0.16 for $C^RC^W$, 0.2 × 0.8 = 0.16 for $C^WC^R$, and thus 0.16 + 0.16 = 0.32, or 32%, for $C^RC^W$ + $C^WC^R$.
- As you can see, the processes of meiosis and random fertilization have maintained the same allele and genotype frequencies that existed in the previous generation.

- The Hardy-Weinberg principle states that the repeated shuffling of a population's gene pool over generations does not increase the frequency of one allele over another.
  - Theoretically, the allele frequencies in our flower population should remain 0.8 for $C^R$ and 0.2 for $C^W$ forever.
- To generalize the example, in a population that has two alleles with frequencies *p* and *q*, the combined frequencies must add to 1, or 100%.
  - Therefore $p + q = 1$.
  - If $p + q = 1$, then $p = 1 - q$ and $q = 1 - p$.
- In the wildflower example, *p* is the frequency of red alleles ($C^R$) and *q* is the frequency of white alleles ($C^W$).
  - The probability of a $C^RC^R$ offspring is $p^2$ (an application of the rule of multiplication).
    - In our example, $p = 0.8$ and $p^2 = 0.64$.
  - The probability of a $C^WC^W$ offspring is $q^2$.
    - In our example, $q = 0.2$ and $q^2 = 0.04$.
  - The probability of a $C^RC^W$ offspring is $2pq$.
    - In our example, $2 \times 0.8 \times 0.2 = 0.32$.
  - The genotype frequencies must add to 1.0: $p^2 + 2pq + q^2 = 1.0$.
    - For the wildflowers, $0.64 + 0.32 + 0.04 = 1.0$.
- This general formula is the **Hardy-Weinberg equation.**
- Using this formula, we can calculate the frequencies of alleles in a gene pool if we know the frequencies of genotypes, or we can calculate the frequencies of genotypes if we know the frequencies of alleles.

***Five conditions must be met for a population to remain in Hardy-Weinberg equilibrium.***

- The Hardy-Weinberg principle describes a hypothetic population that is not evolving. Real populations do evolve, however, and their allele and genotype frequencies *do* change over time.
- Populations evolve because five conditions for non-evolving populations are rarely met for long in nature. A population must satisfy all five conditions to remain in Hardy-Weinberg equilibrium:
  1. **No mutations**. The gene pool is modified if mutations alter alleles or if entire genes are deleted or duplicated.
  2. **Random mating**. If individuals pick mates with certain genotypes, or if inbreeding is common, the mixing of gametes will not be random and genotype frequencies will change.
  3. **No natural selection**. Differential survival or reproductive success among genotypes will alter allele frequencies.
  4. **Extremely large population size**. In small populations, chance fluctuations in the gene pool will cause allele frequencies to change over time, a process called genetic drift.
  5. **No gene flow**. Gene flow, the transfer of alleles due to the migration of individuals or gametes between populations, will change the frequencies of alleles.
- Departure from any of these conditions results in evolutionary change, which is common in natural populations.
  - It is also common for natural populations to be in Hardy-Weinberg equilibrium for specific genes.
  - A population can be evolving at some loci, yet simultaneously be in Hardy-Weinberg equilibrium at other loci.
- The rate of evolutionary change in many populations is so slow that they appear to be close to equilibrium.
  - In such cases, we can use the Hardy-Weinberg equation to estimate genotype and allele frequencies.

***We can apply the Hardy-Weinberg principle to a human population.***

- We can use the Hardy-Weinberg principle to estimate the percent of the human population that carries the allele for the inherited disease phenylketonuria (PKU).
- About one in 10,000 babies born in the United States is born with PKU, a metabolic condition that results in mental retardation and other problems if left untreated.
  - The disease is caused by a recessive allele.
- Newborns are tested for PKU. If they are diagnosed with the disease, their symptoms are lessened with a phenylalanine-free diet.
- Is the U.S. population in Hardy-Weinberg equilibrium with respect to the PKU gene?
  - The mutation rate for the PKU gene is very low. (condition 1)
  - People do not choose their partners based on whether they carry the PKU allele, and inbreeding (marriage to close relatives) is rare in the United States. (condition 2)
  - Selection against PKU acts only against the rare heterozygous recessive individuals, and then only if the dietary restrictions are ignored. As a result, the effects of differential survival and reproductive success among PKU genotypes can be ignored. (condition 3)
  - The U.S. population is very large. (condition 4)
  - Populations outside the United States have PKU allele frequencies similar to those seen in the United States, so gene flow does not alter allele frequencies significantly. (condition 5)
- Because the conditions are met, the population is in Hardy-Weinberg equilibrium.
- From the epidemiologic data, we know that the frequency of homozygous recessive individuals ($q^2$ in the Hardy-Weinberg principle) is one in 10,000, or 0.0001.
  - The frequency of the recessive allele ($q$) is the square root of 0.0001 = 0.01.
  - The frequency of the dominant allele ($p$) is $p = 1 - q$, or $1 - 0.01 = 0.99$.
  - The frequency of carriers (heterozygous individuals) is $2pq = 2 \times 0.99 \times 0.01 = 0.0198$, or about 2%.
- Thus, about 2% of the U.S. population carries the PKU allele.

## Concept 23.3 Natural selection, genetic drift, and gene flow can alter allele frequencies in a population

- Although new mutations can modify allele frequencies, because mutations are rare, the change from generation to generation is very small.
  - Mutation can ultimately have a large effect on allele frequencies when it produces new alleles that strongly influence fitness in a positive or negative way.
- *Nonrandom mating* can affect the frequencies of homozygous and heterozygous genotypes, but it usually has no effect on allele frequencies in the gene pool.
- The three mechanisms that directly alter allele frequencies to bring about evolutionary change are natural selection, genetic drift, and gene flow.

***Natural selection is based on differential survival and reproductive success.***

- Individuals in a population vary in their heritable traits.

- Individuals with variations better suited to the environment tend to produce more offspring than those with variations that are less well suited.
- As a result of selection, alleles are passed on to the next generation in frequencies different from their relative frequencies in the present population.
- For example, the fruit fly *Drosophila melanogaster* has an allele that confers resistance to several insecticides, including DDT.
  - This allele has a frequency of 0% in laboratory strains of *Drosophila* collected in the 1930s, before DDT was used.
  - In strains established after 1960, following 20 years of DDT use, the allele frequency had increased to 37%.
  - The mutation either arose by mutation between 1930 and 1960 or was present in the population, but very rare, prior to 1930.
  - DDT was a strong selective force, favoring alleles that conferred resistance.
- By consistently favoring some alleles over others, natural selection can cause *adaptive evolution* (evolution that results in a better match between organisms and their environment).

***Genetic drift results from chance fluctuations in allele frequencies in small populations.***

- **Genetic drift** occurs when changes in gene frequencies from one generation to another occur because of chance events (sampling errors) that occur in small populations.
  - For example, you would not be too surprised if a tossed coin produced seven heads and three tails in ten tosses, but you would be surprised if you saw 700 heads and 300 tails in 1,000 tosses—you would expect close to 500 of each.
  - The smaller the sample, the greater the chance of deviation from the expected result.
- In a large population, allele frequencies do not change from generation to generation by chance alone.
  - In a small wildflower population with a stable size of only ten plants, however, genetic drift can completely eliminate some alleles.
- Genetic drift in small populations may occur as a result of two situations: the bottleneck effect or the founder effect.
- The **founder effect** occurs when a new population is started by a small number of individuals who do not represent the gene pool of the larger source population.
  - At an extreme, a population could be started by a single pregnant female or a single seed with only a tiny fraction of the genetic variation of the source population.
- Genetic drift continues from generation to generation until the population grows large enough for sampling errors to be minimal.
- Founder effects have been demonstrated in human populations that started from a small group of colonists.
- The **bottleneck effect** occurs when the numbers of individuals in a large population are drastically reduced by a disaster.
  - By chance, some alleles may be overrepresented and others underrepresented among the survivors. Some alleles may be eliminated altogether.
- Genetic drift continues to change the gene pool until the population is large enough to eliminate the effect of chance fluctuations.
- The bottleneck effect is an important concept in conservation biology of endangered species.

- Genetic drift has played an important role in the conservation of the greater prairie chicken *(Tympanuchus cupido).*
  - Millions of greater prairie chickens once lived on the prairies of Illinois.
  - By 1993, only two populations of birds remained in Illinois, together totaling fewer than 50 birds.
  - The few surviving birds had low levels of genetic variation. Less than 50% of the eggs hatched, compared to higher hatching rates of larger populations in other states.
- These data suggest that genetic drift during the bottleneck may have led to a loss of genetic variation and an increase in the frequency of deleterious alleles.
- Juan Bouzat and his colleagues extracted DNA from 165 museum specimens of Illinois greater prairie chickens.
  - Ten of the birds were collected in the 1930s, when the Illinois population was 25,000.
  - Five were collected in the 1960s, when the population was 1,000.
  - The researchers surveyed six loci and found that the small 1993 population had lost nine alleles present in the museum specimens.
- To counter the negative effects of genetic drift, the researchers brought in 271 birds from neighboring states.
  - New alleles entered the Illinois population, and the egg-hatching rate improved to greater than 90%.
- This example highlights four key points about genetic drift.
  1. Genetic drift is significant in small populations.
  2. Genetic drift causes allele frequencies to change at random.
  3. Genetic drift leads to a loss of genetic variation within populations.
  4. Genetic drift can cause harmful alleles to become fixed.

***A population may lose or gain alleles by gene flow.***

- **Gene flow** is the transfer of alleles among populations due to the migration of fertile individuals or gametes.
  - For example, if a nearby wildflower population consisted entirely of white flowers, its pollen ($C^W$ alleles only) could be carried into our hypothetical population.
  - The result would be an increase the frequency of $C^W$ alleles in the hypothetical population in the next generation.
- Gene flow tends to reduce differences between populations.
  - If extensive enough, gene flow can combine neighboring populations into a single population with a common gene pool.
- Alleles transferred by gene flow can also affect how well populations are adapted to local environmental conditions.
  - Two populations of the songbird *Parus major*, the great tit, live on the small Dutch island of Vlieland.
  - Researchers have noted survival differences between the two populations on the island.
  - Females born in the eastern population survived twice as well as females born in the central population, regardless of where the females eventually settled and raised offspring. This suggests that females born in the east are better adapted to life on the island than females born in the central population.
  - The two populations are connected by high levels of gene flow (mating), indicating there should be few genetic differences between them.

- How can the eastern population be better adapted to life on Vlieland than the central population?
  - The answer lies in the unequal amounts of gene flow from the mainland.
  - In any given year, 43% of the first-time breeders in the central population were immigrants from the mainland, compared to only 13% in the eastern population.
  - Birds with mainland genotypes survive and reproduce poorly on Vlieland, and in the eastern population, selection reduces the frequency of these genotypes.
  - In the central population, gene flow from the mainland is so high that it overwhelms the effects of selection.
  - As a result, females born in the west have many immigrant genes, thereby reducing the degree to which members of that population are adapted to life on the island.
- Beneficial alleles can also be transferred between populations.
  - For example, gene flow has resulted in the worldwide spread of insecticide-resistance alleles in the mosquito *Culex pipiens*, a vector of West Nile virus.
- Gene flow is an increasingly important agent of evolutionary change in human populations.
  - With increased human mobility, mating is more common between previously isolated populations, leading to an exchange of alleles and reducing genetic differences between human populations.

## Concept 23.4 Natural selection is the only mechanism that consistently causes adaptive evolution

- Evolution by natural selection is a blend of chance and “sorting”: chance in the creation of new genetic variations (as in mutation) and sorting as natural selection favors some alleles over others.
  - Because of this favoring process, the outcome of natural selection is *not* random.
  - Of all the factors that can change a gene pool, only natural selection leads to the adaptation of an organism to its environment.
- The terms “struggle for existence” and “survival of the fittest” are misleading because they suggest that individuals compete directly in contests.
- In some animal species, males *do* compete directly for mates.
- Reproductive success is generally subtler, however, and depends on factors other than the battle for mates.
  - For example, a barnacle may produce more eggs than its neighbors because it is more efficient at filtering food from the water.
  - A moth may have more offspring than its competitors because its body colors conceal it from predators, allowing it to survive long enough to reproduce.
- These examples illustrate how adaptive advantage can lead to greater **relative fitness**: the contribution an individual makes to the gene pool of the next generation, *relative* to the contributions of other individuals.
- Although we may refer to the relative fitness of a genotype, the entity that is subjected to natural selection is the whole organism, not the underlying genotype.
  - Natural selection acts on the genotype indirectly, via how the genotype affects the phenotype.

### *There are three modes of selection: directional, disruptive, and stabilizing.*

- Natural selection can alter the frequency distribution of heritable traits in three ways, depending on which phenotypes in a population are favored.
- The three modes of selection are called directional, disruptive, and stabilizing selection.

- **Directional selection** is most common during periods of environmental change or when members of a population migrate to a new habitat with different environmental conditions.
- Directional selection shifts the frequency curve for a phenotypic character in one direction by favoring individuals who deviate from the average.
  - For example, an increase in the size of seeds available as food led to an increase in beak depth in a population of Galápagos finches.
- **Disruptive selection** occurs when environmental conditions favor individuals at both extremes of the phenotypic range over those with intermediate phenotypes.
  - For example, two distinct bill types are present in Cameroon's black-bellied seedcrackers.
  - Larger-billed birds are more efficient in feeding on hard seeds, and smaller-billed birds are more efficient in feeding on soft seeds.
  - Birds with intermediate bills are relatively inefficient at cracking both types of seeds and thus have lower relative fitness.
- **Stabilizing selection** favors intermediate variants and acts against extreme phenotypes.
- Stabilizing selection reduces variation and maintains the status quo for a trait.
  - Human birth weight is subject to stabilizing selection.
  - Babies much larger or smaller than 3–4 kg have higher infant mortality than average-sized babies.

***Natural selection plays a key role in adaptive evolution.***

- The adaptations of organisms are essential to their survival and reproductive success.
  - Natural selection increases the frequencies of alleles that enhance survival and reproduction.
  - As the proportion of individuals that have favorable characteristics increases over time, the match between a species and its environment improves, and adaptive evolution occurs.
- Because the physical and biological components of an organism's environment may change, adaptive evolution is a continuous, dynamic process.
- Natural selection is the only evolutionary mechanism that consistently leads to adaptive evolution.
  - Genetic drift can cause the frequency of a slightly beneficial allele to increase, but it also can cause the frequency of such an allele to decrease.
  - Similarly, gene flow may introduce alleles that are advantageous or ones that are disadvantageous.

***Sexual selection may lead to pronounced secondary differences between the sexes.***

- Charles Darwin was the first scientist to investigate **sexual selection***,* which is selection for mating success.
- Sexual selection results in **sexual dimorphism**, a difference between the sexes in secondary sexual characteristics such as size, coloration, and ornamentation.
- It is important to distinguish between *intra*sexual and *inter*sexual selection.
- **Intrasexual selection** is direct competition among individuals of one sex for mates of the opposite sex.
  - Competition may take the form of direct physical battles between individuals, usually males.
  - For example, a single male may patrol a group of females and prevent other males from mating with them.
  - More commonly, ritualized displays discourage lesser competitors and determine dominance.

- Intrasexual selection has been observed among females in several species, including ring-tailed lemurs and broad-nosed pipefish.
- **Intersexual selection**, or *mate choice*, occurs when members of one sex (usually females) are choosy in selecting their mates from individuals of the other sex.
    - Because females invest more in eggs and parental care, they are choosier about their mates than males.
    - A female tries to select a mate that will confer a fitness advantage on their mutual offspring.
    - In many cases, the female chooses a male based on his showy appearance or behavior.
- Some male showiness does not seem to be adaptive except in attracting mates and may even put the male at considerable risk.
    - For example, bright plumage may make male birds more visible to predators.
    - Even if these extravagant features have some costs, an individual that possess them will have enhanced fitness if they help that individual gain a mate.
    - Every time a female chooses a mate based on appearance or behavior, she perpetuates the alleles that caused her to make that choice.
    - She also enables a male with that particular phenotype to perpetuate his alleles.
- How do female preferences for certain male characteristics evolve? Are there fitness benefits to showy traits?
    - Several researchers are testing the hypothesis that females use male sexual advertisements to measure the male's overall health and immune function.
    - Males with serious parasitic infections may have dull, disheveled plumage. These individuals are unlikely to win many females.
    - If a female chooses a showy mate, she may be choosing a healthy one, and her benefit is a greater probability of having healthy offspring.

***Balancing selection preserve genetic variation.***

- **Balancing selection** occurs when natural selection maintains stable frequencies of two or more phenotypes in a population.
- One mechanism that produces balanced polymorphism is **heterozygote advantage**.
    - In some situations, individuals who are heterozygous at a particular locus have greater fitness than homozygotes.
    - In these cases, natural selection will maintain multiple alleles at that locus.
- Heterozygote advantage is defined in terms of the *genotype*, not the phenotype.
    - Whether heterozygote advantage represents stabilizing or directional selection depends on the relationship between genotype and phenotype.
    - If the phenotype of a heterozygote is intermediate to the phenotypes of both homozygotes, then heterozygote advantage is a form of stabilizing selection.
- Heterozygote advantage maintains genetic diversity at the human gene for the ß polypeptide subunit chain of hemoglobin.
    - A recessive allele at that locus causes sickle-cell disease.
    - Homozygous recessive individuals suffer from sickle-cell disease. Homozygous dominant individuals are vulnerable to malaria. Heterozygous individuals are resistant to malaria.
- The red blood cells of people with sickle-cell disease become *sickled* under low oxygen conditions.

    - The sickled cells can clump together and block blood flow in the capillaries, damaging organs like the kidney, heart, and brain.
    - Some red blood cells become sickled in heterozygotes, but not enough to cause sickle-cell disease.
- Heterozygotes are protected against the most serious effects of malaria, as the body destroys sickled red blood cells and kills the parasites they harbor.
- The frequency of the sickle-cell allele is highest in areas where the malarial parasite is common.
    - In some African populations, the sickle-cell allele accounts for 20% of the gene pool, a very high frequency for such a harmful allele.
- A second mechanism that promotes balanced polymorphism is **frequency-dependent selection**.
    - Frequency-dependent selection occurs when the fitness of any one morph declines if it becomes too common in the population.
    - Frequency-dependent selection has been observed in a number of predator-prey interactions in the wild.

***Natural selection cannot fashion perfect organisms.***

- There are at least four reasons natural selection cannot produce perfection.
    1. **Selection can act only on existing variations.**
    - Natural selection favors only the fittest phenotypes among those currently in the population, which may not be the ideal traits.
    - New advantageous alleles do not arise on demand.
    2. **Evolution is limited by historical constraints.**
    - Evolution does not scrap ancestral features and build new complex structures or behavior from scratch.
    - Evolution co-opts existing features and adapts them to new situations.
    - For example, birds might benefit from having wings plus four legs. However, birds descended from reptiles that had only two pairs of limbs. Co-opting the forelimbs for flight left only two hind limbs for movement on the ground.
    3. **Adaptations are often compromises.**
    - Each organism must do many different things.
    - Because the flippers of a seal must allow it to walk on land and also swim efficiently, their design is a compromise between these environments.
    - Human limbs are flexible and allow versatile movements but are prone to injuries, such as sprains, torn ligaments, and dislocations.
    - Better structural reinforcement of human limbs would compromise their agility.
    4. **Chance, natural selection, and the environment interact**.
    - Chance events affect the subsequent evolutionary history of populations.
    - For example, the founders of new populations may not necessarily be the individuals best suited to the new environment, but rather those individuals that were carried there by chance.
- With these constraints, evolution does not tend to craft perfect organisms.
    - In fact, the evidence for evolution can be seen in the many imperfections of the organisms it produces.