**Chapter 23 The Evolution of Populations**

**Lecture Outline**

Overview: The Smallest Unit of Evolution

•One common misconception about evolution is that organisms evolve, in a Darwinian sense, during their lifetimes.

•Natural selection does act on individuals. Each individual’s combination of inherited traits affects its survival and its reproductive success relative to other individuals in the population.

•However, the evolutionary impact of natural selection is only apparent in the changes in a population of organisms over time.

•It is the population, not the individual, that evolves.

•Consider the example of bent grass (Agrostis tenuis) growing on the tailings of an abandoned mine. These tailings are rich in toxic heavy metals.

•While many bent grass seeds land on the mine tailings each year, the only plants that germinate, grow, and reproduce are those that possess genes enabling them to tolerate metallic soils.

•These plants tend to produce metal-tolerant offspring.

•Individual plants do not evolve to become more metal-tolerant during their lifetimes.

**Concept 23.1** Population genetics provides a foundation for studying evolution

•Darwin proposed a mechanism for change in species over time.

•What was missing from Darwin’s explanation was an understanding of inheritance that could explain how chance variations arise in a population while also accounting for the precise transmission of these variations from parents to offspring.

•The widely accepted hypothesis of the time—that the traits of parents are blended in their offspring—would eliminate the differences in individuals over time.

•Just a few years after Darwin published On 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 Gregor Mendel and Charles Darwin were contemporaries, Darwin never saw Mendel’s paper, and its implications were not understood by the few scientists who did read it at the time.

•Mendel’s contribution to evolutionary theory was not appreciated until half a century later.

The modern evolutionary synthesis integrated Darwinian selection and Mendelian inheritance.

•When Mendel’s research was rediscovered in the early 20th century, many geneticists believed that his laws of inheritance conflicted with Darwin’s theory of natural selection.

•Darwin emphasized quantitative characters, those that vary along a continuum.

•These characters are influenced by multiple loci.

•Mendel and later geneticists investigated discrete “either-or” traits.

•It was not obvious that there was a genetic basis to quantitative characters.

•Within a few decades, geneticists determined that quantitative characters are influenced by multiple genetic loci and that the alleles at each locus follow Mendelian laws of inheritance.

•These discoveries helped reconcile Darwin’s and Mendel’s ideas and led to the birth of population genetics, the study of how populations change genetically over time.

•A comprehensive theory of evolution, the modern synthesis, took form in the early 1940s.

•It integrated discoveries and ideas from paleontology, taxonomy, biogeography, and population genetics.

•The first architects of the modern synthesis included statistician R. A. Fisher, who demonstrated the rules by which Mendelian characters are inherited, and biologist J. B. S. Haldane, who explored the rules of natural selection. Later contributors included geneticists Theodosius Dobzhansky and Sewall Wright, biogeographer and taxonomist Ernst Mayr, paleontologist George Gaylord Simpson, and botanist G. Ledyard Stebbins.

•The modern synthesis emphasizes:

•The importance of populations as the units of evolution.

•The central role of natural selection as the most important mechanism of adaptive evolution.

•The idea of gradualism to explain how large changes can evolve as an accumulation of small changes over long periods of time.

•While many evolutionary biologists are now challenging some of the assumptions of the modern synthesis, it has shaped our ideas about how populations evolve.

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

•A population is a localized group of individuals that belong to the same species.

•One definition of a species is a group of natural populations whose individuals have the potential to interbreed and produce fertile offspring.

•Populations of a species may be isolated from each other and rarely exchange genetic material.

•Members of a population are far more likely to breed with members of the same population than with members of other populations.

•Individuals near the population’s center are, on average, more closely related to one another than to members of other populations.

•The total aggregate of genes in a population at any one time is called the population’s gene pool.

•It consists of all alleles at all gene loci in all individuals of a population.

•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 for a particular locus, then individuals can be either homozygous or heterozygous for that gene.

•Each allele has a frequency in the population’s gene pool.

•For example, imagine a population of 500 wildflower plants with two alleles (CR and CW) at a locus that codes for flower pigment.

•Suppose that in the imaginary population of 500 plants, 20 (4%) are homozygous for the CW allele (CWCW) and have white flowers.

•Of the remaining plants, 320 (64%) are homozygous for the CR allele (CRCR) and have red flowers.

•These alleles show incomplete dominance. 160 (32%) of the plants are heterozygous (CRCW) 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 (CR) accounts for 800 copies (320 × 2 for CRCR + 160 × 1 for CRCW).

•The frequency of the CR allele in the gene pool of this population is 800/1,000 = 0.8, or 80%.

•The CW 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 CR allele in this population, is 0.8.

•The frequency of the CW allele, represented by q, is 0.2.

The Hardy-Weinberg Theorem describes a nonevolving population.

•The Hardy-Weinberg theorem describes the gene pool of a nonevolving population.

•This theorem 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.

•In our imaginary wildflower population of 500 plants, 80% (0.8) of the flower color alleles are CR, and 20% (0.2) are CW.

•How will meiosis and sexual reproduction affect the frequencies of the two alleles in the next generation?

•We assume that fertilization is completely random and all male-female mating combinations are equally likely.

•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 an CR allele and a 0.2 chance of bearing an CW 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, we can determine the frequencies of the three possible genotypes in the next generation.

•The probability of picking two CR alleles (to obtain a CRCR genotype) is 0.8 × 0.8 = 0.64, or 64%.

•The probability of picking two CW alleles (to obtain a CWCW genotype) is 0.2 × 0.2 = 0.04, or 4%.

•Heterozygous individuals are either CRCW or CWCR, depending on whether the CR allele arrived via sperm or egg.

•The probability of being heterozygous (with a CRCW genotype) is 0.8 × 0.2 = 0.16 for CRCW, 0.2 × 0.8 = 0.16 for CWCR, and 0.16 + 0.16 = 0.32, or 32%, for CRCW + CWCR.

•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 theorem 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 at 0.8 for CR and 0.2 for CW forever.

•To generalize the example, in a population with two alleles with frequencies of p and q, the combined frequencies must add to 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 (CR) and q is the frequency of white alleles (CW).

•The probability of generating an CRCR offspring is p2 (an application of the rule of multiplication).

•In our example, p = 0.8 and p2 = 0.64.

•The probability of generating a CWCW offspring is q2.

•In our example, q = 0.2 and q2 = 0.04.

•The probability of generating a CRCW offspring is 2pq.

•In our example, 2 × 0.8 × 0.2 = 0.32.

•The genotype frequencies must add up to 1.0:

p2 + 2pq + q2 = 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 frequencies of alleles in a gene pool if we know the frequency of genotypes, or the frequency 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 theorem describes a hypothetic population that is not evolving. However, real populations do evolve, and their allele and genotype frequencies do change over time.

•That is because the five conditions for nonevolving populations are rarely met for long in nature.

•A population must satisfy five conditions if it is to remain in Hardy-Weinberg equilibrium: 1.Extremely large population size. In small populations, chance fluctuations in the gene pool can cause genotype frequencies to change over time. These random changes are called genetic drift.

2.No gene flow. Gene flow, the transfer of alleles due to the migration of individuals or gametes between populations, can change the proportions of alleles.

3.No mutations. Introduction, loss, or modification of genes will alter the gene pool.

4.Random mating. If individuals pick mates with certain genotypes, or if inbreeding is common, the mixing of gametes will not be random.

5.No natural selection. Differential survival or reproductive success among genotypes will alter their frequencies.

•Evolution usually results when any of these five conditions are not met.

•Although natural populations are rarely, if ever, in true Hardy-Weinberg equilibrium, 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 use the theorem to estimate the percentage of the human population that carries the allele for the inherited disease phenylketonuria (PKU).

•About 1 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.

•Is the U.S. population in Hardy-Weinberg equilibrium with respect to the PKU gene? 1.The U.S. population is very large.

2.Populations outside the United States have PKU allele frequencies similar to those seen in the United States, so gene flow will not alter allele frequencies significantly.

3.The mutation rate for the PKU gene is very low.

4.People do not choose their partners based on whether or not they carry the PKU allele, and inbreeding (marriage to close relatives) is rare in the United States.

5.Selection against PKU only acts against the rare heterozygous recessive individuals.

•From the epidemiological data, we know that frequency of homozygous recessive individuals (q2 in the Hardy-Weinberg theorem) = 1 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 × 0.99 × 0.01 = 0.0198, or about 2%.

•Thus, about 2% of the U.S. population carries the PKU allele.

**Concept 23.2** Mutation and sexual recombination produce the variation that makes evolution possible

New genes and new alleles originate only by mutation.

•A mutation is a change in the nucleotide sequence of an organism’s DNA.

•Most mutations occur in somatic cells and are lost when the individual dies.

•Only mutations in cell lines that form gametes can be passed on to offspring, and only a small fraction of these spread through populations and become fixed.

•A new mutation that is transmitted in a gamete to an offspring can immediately change the gene pool of a population by introducing a new allele.

•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.

•However, most point mutations are harmless.

•Much of the DNA in eukaryotic genomes does not code for protein products.

•However, some noncoding regions of DNA do regulate gene expression.

•Changes in these regulatory regions of DNA can have profound effects.

•Because the genetic code is redundant, some point mutations in genes that code for proteins may not alter the protein’s amino acid composition.

•On rare occasions, a mutant allele may actually make its bearer better suited to the environment, increasing reproductive success.

•This is more likely when the environment is changing.

•Some mutations alter gene number or sequence.

•Chromosomal mutations that delete or rearrange many gene loci at once are almost always 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 to positive effect.

•Gene duplication is an important source of new genetic variation.

•Small pieces of DNA can be introduced into the genome through the activity of transposons.

•Such duplicated segments can persist over generations and provide new loci that may eventually take on new functions by mutation and subsequent selection.

•New genes may also arise when the coding subsections of genes known as exons are shuffled within the genome, within a single locus or between loci.

•Such 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 though various mutational mechanisms.

•Modern humans have close to 1,000 olfactory receptor genes.

•60% of these genes have been inactivated in humans, due to mutations.

•Mice, who rely more on their sense of smell, have lost only 20% of their olfactory receptor genes.

•Mutation rates vary from organism to organism.

•Mutation rates are low in animals and plants, averaging about 1 mutation in every 100,000 genes per generation.

•In microorganisms and viruses with short generation spans, mutation rates are much higher and can rapidly generate genetic variation.

Sexual recombination also produces genetic variation.

•On a generation-to-generation timescale, sexual recombination is far more important than mutation in producing the genetic differences that make adaptation possible.

•Sexual reproduction rearranges alleles into novel combinations every generation.

•Bacteria and viruses can also undergo recombination, but they do so less regularly than animals and plants.

•Bacterial and viral recombination may cross species barriers.

**Concept 23.3** Natural selection, genetic drift, and gene flow can alter a population’s genetic composition

•Although new mutations can modify allele frequencies, the change from generation to generation is very small.

•Recombination reshuffles alleles but does not change their frequency.

•Three major factors alter allele frequencies to bring about evolutionary change: natural selection, genetic drift, and gene flow.

Natural selection is based on differential reproductive success.

•Individuals in a population vary in their heritable traits.

•Those 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.

•Imagine that in our imaginary wildflower population, white flowers are more visible to herbivorous insects and thus have lower survival. Imagine that red flowers are more visible to pollinators.

•Such differences in survival and reproductive success would disturb the Hardy-Weinberg equilibrium. The frequency of the CW allele would decline and the frequency of the CR allele would increase.

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 thrown 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 will not change from generation to generation by chance alone.

•However, in a small wildflower population with a stable size of only ten plants, genetic drift can completely eliminate some alleles.

•Genetic drift at small population sizes may occur as a result of two situations: the bottleneck effect or the founder effect.

•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 will continue 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.

•Populations that have suffered bottleneck incidents have lost genetic variation from the gene pool.

•This reduces individual variation and may reduce adaptation.

•For example, in the 1890s, hunters reduced the population of northern elephant seals in California to 20 individuals.

•Now that it is a protected species, the population has increased to more than 30,000.

•However, a study of 24 gene loci in a representative sample of seals showed no variation. One allele had been fixed for each gene.

•Populations of the closely related southern elephant seal, which did not go through a bottleneck, show abundant genetic variation.

•The founder effect occurs when a new population is started by only a few 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 single seed with only a tiny fraction of the genetic variation of the source population.

•Genetic drift would continue from generation to generation until the population grew large enough for sampling errors to be minimal.

•Founder effects have been demonstrated in human populations that started from a small group of colonists.

A population may lose or gain alleles by gene flow.

•Gene flow is genetic exchange due to migration of fertile individuals or gametes between populations.

•For example, if a nearby wildflower population consisted entirely of white flowers, its pollen (CW alleles only) could be carried into our target population.

•This would increase the frequency of CW alleles in the target population in the next generation.

•Gene flow tends to reduce differences between populations.

•If extensive enough, gene flow can amalgamate neighboring populations into a single population with a common gene pool.

•Humans today migrate much more freely than in the past, and gene flow has become an important agent of evolutionary change in human populations that were previously isolated.

**Concept 23.4** Natural selection is the primary mechanism of adaptive evolution

•Of all the factors that can change a gene pool, only natural selection leads to adaptation of an organism to its environment.

•Natural selection accumulates and maintains favorable genotypes in a population.

•Most populations have extensive genetic variation.

•Not all variation is heritable. For example, body builders alter their phenotypes but do not pass on their huge muscles to their children.

•Only the genetic component of variation can have evolutionary consequences as a result of natural selection.

•This is because only heritable traits pass from generation to generation.

Genetic variation occurs within and between populations.

•Both quantitative and discrete characters contribute to variation within a population.

•Quantitative characters are those that 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.

•Discrete characters, such as flower color, are usually determined by a single locus with different alleles that produce distinct phenotypes.

•Phenotypic polymorphism occurs when two or more discrete phenotypes are represented in high enough frequencies to be noticeable in a population.

•The contrasting forms are called morphs, as in the red-flowered and white-flowered morphs in our wildflower population.

•Human populations are polymorphic for a variety of physical (e.g., freckles) and biochemical (e.g., blood types) characters.

•Polymorphism applies only to discrete characters, not quantitative characters.

•Human height, which varies in a continuum, is not a phenotypic polymorphism.

•Population geneticists measure genetic variation by determining the amount of heterozygosity at the level of whole genes (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 13,000 gene loci are homozygous (fixed).

•About 14% (1,800 genes) are heterozygous.

•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.

•Why does average heterozygosity tend to be greater than nucleotide diversity?

•This is 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.

•Humans have relatively little genetic variation.

•Nucleotide diversity is only 0.1%.

•You and your neighbor probably have the same nucleotide at 999 out of every 1,000 nucleotide sites in your DNA.

•Geographic variation results from differences in phenotypes or genotypes between populations or between subgroups of a single population that inhabit different areas.

•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 can occur on a local scale, within a population, if the environment is patchy or if dispersal of individuals is limited, producing subpopulations. This is termed spatial variation.

•Geographic variation in the form of graded change in a trait along a geographic axis is called a cline.

•Clines may represent intergrade zones where individuals from neighboring, genetically different, populations interbreed.

•Alternatively, clines may reflect the influence of natural selection based on gradation in some environmental variable.

•For example, the average body size of many North American species of birds and mammals increases gradually with increasing latitude, allowing Northern populations to conserve heat in cold environments by decreasing the ratio of surface area to volume.

Let’s take a closer look at natural selection.

•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 and depends on factors other than 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.

•Wildflowers may be successful because they attract more pollinators.

•These examples of adaptive advantage are all components of evolutionary fitness.

•Fitness is defined as the contribution an individual makes to the gene pool of the next generation, relative to the contributions of other individuals.

•Population geneticists define relative fitness as the contribution of a genotype to the next generation compared to the contribution of alternative genotypes for the same locus.

•Consider our wildflower population.

•Let’s assume that individuals with red flowers produce fewer offspring than those with white or pink flowers, which produce equal numbers of offspring.

•The relative fitness of the most successful variants is set at 1.0 as a basis for comparison, so the relative fitness of white (CWCW) and pink (CRCW) plants is 1.0.

•If plants with red flowers (CRCR) produce only 80% as many offspring, their relative fitness is 0.8.

•Although population geneticists measure the relative fitness of a genotype, it is important to remember that natural selection acts on phenotypes, not genotypes.

•The whole organism is subjected to natural selection.

•The relative fitness of an allele depends on the entire genetic and environmental context in which it is expressed.

•Survival alone does not guarantee reproductive success.

•Relative fitness is zero for a sterile organism, even if it is robust and long-lived.

•On the other hand, longevity may increase fitness if long-lived individuals leave more offspring than short-lived individuals.

•In many species, individuals that mature quickly, become fertile at an early age, and live for a short time have greater relative fitness than individuals that live longer but mature later.

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, fossil evidence indicates that the average size of black bears in Europe increased during each glacial period, only to decrease again during the warmer interglacial periods.

•Large bears have a smaller surface-to-volume ratio and are better at conserving body heat during periods of extreme cold.

•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.

•Disruptive selection can be important in the early stages of speciation.

•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.

Diploidy and balancing selection preserve genetic variation.

•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 only exposed to selection 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.

•Balancing selection occurs when natural selection maintains stable frequencies of two or more phenotypes in a population, a state called balanced polymorphism.

•One mechanism producing 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.

•Heterozygous advantage maintains genetic diversity at the human gene for one chain of hemoglobin.

•Homozygous recessive individuals suffer from sickle-cell disease.

•Homozygous dominant individuals are vulnerable to malaria.

•Heterozygous individuals are resistant to malaria.

•The frequency of the sickle-cell allele is highest in areas where the malarial parasite is common.

•In some African tribes, it accounts for 20% of the gene pool, a very high frequency for such a harmful allele.

•Even at this high frequency, only 4% of the population suffers from sickle-cell disease (q2 = 0.2 × 0.2 = 0.04), while 32% of the population is resistant to malaria (2pq = 2 × 0.8 × 0.2 = 0.32).

•The aggregate benefit of the sickle-cell allele in the population balances its aggregate harm.

•A second mechanism promoting 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.

•Predators may develop “search images” of the most common forms of prey. A prey morph that becomes too common may become disproportionately vulnerable to predation.

•Frequency-dependent selection has been observed in a number of predator-prey interactions in the wild.

•Some genetic variations, neutral variations, have negligible impact on fitness, and thus natural selection does not affect these alleles.

•For example, the diversity of human fingerprints seems to confer no selective advantage to some individuals over others.

•Most of the base differences between humans that are found in untranslated parts of the genome appear to confer no selective advantage.

•Pseudogenes, genes that have become inactivated by mutations, accumulate genetic variations.

•Over time, some neutral alleles will increase and others will decrease by the chance effects of genetic drift.

•There is no consensus among biologists on how much genetic variation can be classified as neutral or even if any variation can be considered truly neutral.

•It is almost impossible to demonstrate that an allele brings no benefit at all to an organism.

•Also, variant alleles may be neutral in one environment but not in another.

•Even if only a fraction of the extensive variation in a gene pool significantly affects an organism, there is still an enormous reservoir of raw material for natural selection and adaptive evolution.

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

•Charles Darwin was the first scientist to investigate sexual selection, which is natural selection for mating success.

•Sexual selection results in sexual dimorphism, marked differences between the sexes in secondary sexual characteristics not directly associated with reproduction.

•Males and females may differ in size, coloration, and ornamentation.

•In vertebrates, males are usually the larger and showier sex.

•It is important to distinguish between intrasexual and intersexual selection.

•Intrasexual selection is direct competition among individuals of one sex (usually males) for mates of the opposite sex.

•Competition may take the form of direct physical battles between individuals.

•The stronger individuals gain status.

•More commonly, ritualized displays discourage lesser competitors and determine dominance.

•Evidence is growing that intrasexual selection can take place between females as well.

•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 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, individuals that possess them will have enhanced fitness if they help an 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 allows 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.

•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.

Sex is an evolutionary enigma.

•As a mechanism of rapid population growth, sex is far inferior to asexual reproduction.

•Consider a population in which half the females reproduce only asexually and half the females reproduce only sexually.

•Assume that both types of females produce equal numbers of offspring each generation.

•The asexual condition will increase in frequency, because: •All offspring of asexual females will be reproductive daughters.

•? Only half of the offspring of sexual females will be daughters; the other half will necessarily be males.

•Sex is maintained in the vast majority of eukaryotic species, even those that also reproduce asexually.

•Sex must confer some selective advantage to compensate for the costs of diminished reproductive output.

•Otherwise, migration of asexual individuals or mutation permitting asexual reproduction would outcompete sexual individuals and the alleles favoring sex.

•The traditional explanation for the maintenance of sex was that the process of meiosis and fertilization generate genetic variation on which natural selection can act.

•However, the assumption that sex is maintained in spite of its disadvantages because it produces future adaptation in a variable world is difficult to defend.

•Natural selection acts in the present, favoring individuals here and now that best fit the current, local environment.

•Let us instead consider how the genetic variation promoted by sex might be advantageous in the short term, on a generation-to-generation timescale.

•Genetic variability may be important in resistance to disease.

•Parasites and pathogens recognize and infect their hosts by attaching to receptor molecules on the host’s cells.

•There should be an advantage to producing offspring that vary in their resistance to different diseases.

•One offspring may have cellular markers that make it resistant to virus A, while another is resistant to virus B.

•This hypothesis predicts that gene loci that code for receptors to which pathogens attack should have many alleles.

•In humans, there are hundreds of alleles for each of two gene loci that give cell surfaces their molecular fingerprints.

•At the same time, parasites evolve very rapidly in their ability to use specific host receptors.

•However, sex provides a mechanism for changing the distribution of alleles and varying them among offspring.

•This coevolution in which host and parasite must evolve quickly to keep up with each other has been called a “Red Queen race.”

Natural selection cannot fashion perfect organisms.

•There are at least four reasons natural selection cannot produce perfection. 1.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.

2.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.

•Similarly, human limbs are flexible and allow versatile movements, but are prone to injuries, such as sprains, torn ligaments, and dislocations.

•Better structural reinforcement would compromise agility.

3.Chance and natural selection interact. •Chance events affect the subsequent evolutionary history of populations.

•For example, 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.

4.Selection can only edit existing variations. •Natural selection favors only the fittest variations from those phenotypes that are available.

•New alleles do not arise on demand.

•Natural selection works by favoring the best variants available.

•The many imperfections of living organisms are evidence for evolution.