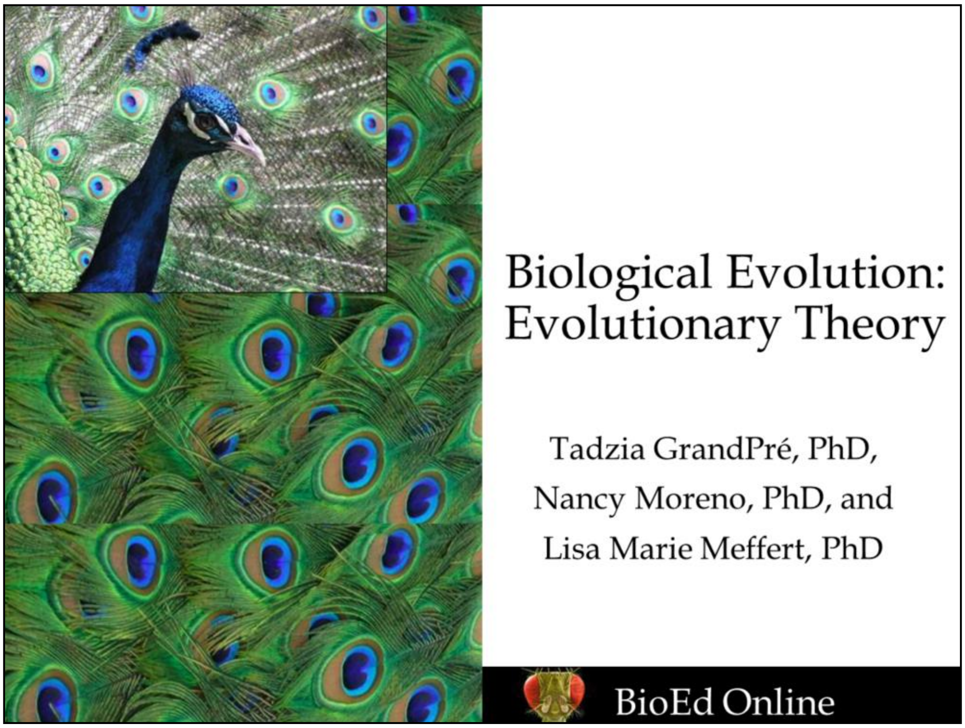
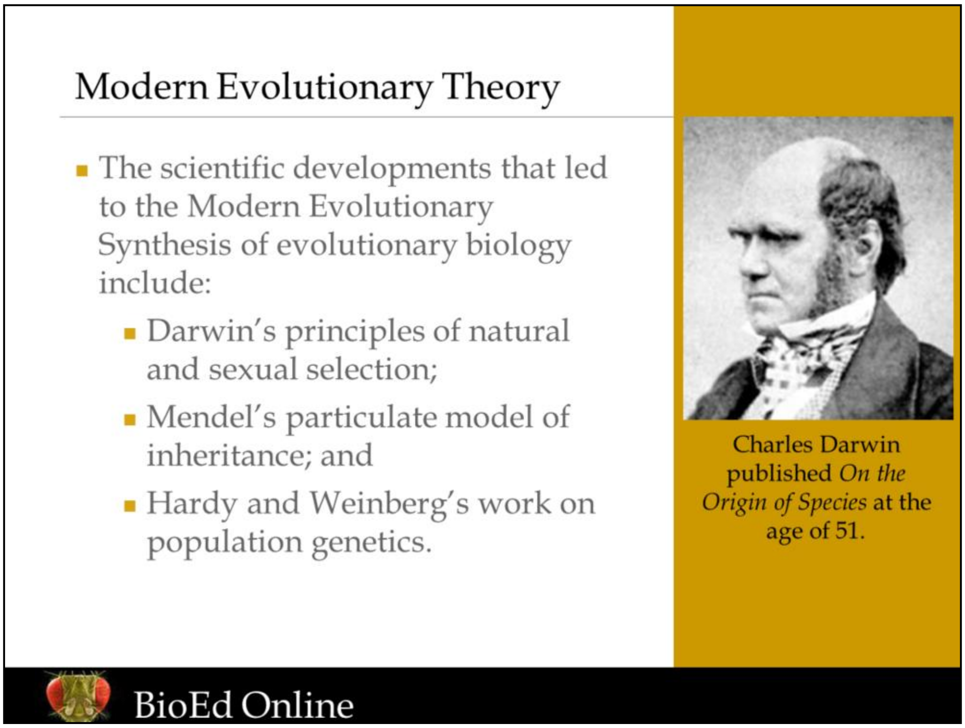


Biological Evolution is a basic overview of evolutionary theory.

Image References:
Wikimedia Commons. (2006). Peacock closeup (Julie Slama). Retrieved 2-3-09 from, http://commons.wikimedia.org/wiki/File:040411.JPG.



Modern Evolutionary Theory

By the early 19th century, scientists had gathered enough evidence to recognize that living creatures had existed on Earth for a long time and that life had changed and diversified since its origin. However, they did not understand the processes or mechanisms that drive biological diversity (variation in life forms), or how physical traits are inherited (passed on) from one generation to the next. One of the prevailing ideas was that of "blending inheritance," which posits that offspring should look like some mixture of the two parents. While this principle had some merit, it did not explain how variation persists in different populations over time. Under the blending inheritance model, all individuals within a given population eventually should end up looking alike. Clearly, this is not seen in nature.

With the publication of "*On the Origin of Species"* in 1859, Charles Darwin changed the way naturalists and other scientists thought about the diversity seen in nature. Darwin hypothesized that all living things are descendants of one or a few common ancestors and that diversity arises through the process of evolution, which is driven by natural and sexual selection.

Darwin described how natural and sexual selection caused variation to arise in nature, but the genetic mechanisms underlying these processes still were not understood. It was Gregor Mendel, an Augustinian monk who was working around the same time as Darwin, who solved this part of the puzzle. Through his experiments on pea plants, Mendel arrived at a model of "particulate inheritance" that explained how variation can be inherited and maintained over time.

Statistical models developed by G.H. Hardy and Wilhelm Weinberg helped to merge and fill out Darwin's and Mendel's observations into what is often referred to as "The Modern Synthesis" of evolutionary theory. This presentation covers these topics in detail.

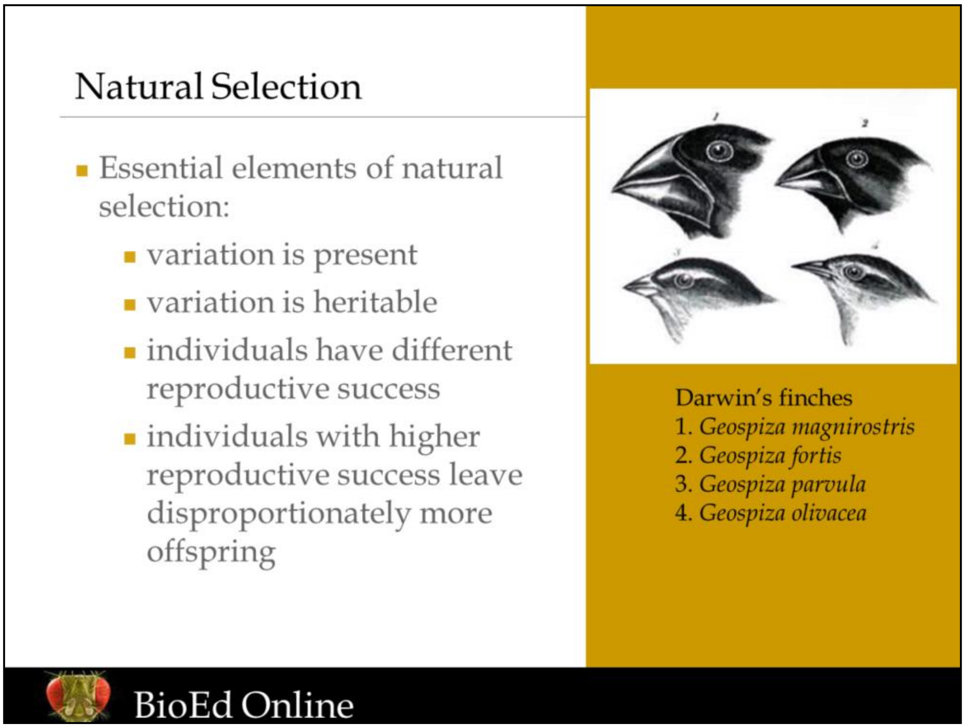
Note: in lay terminology, the word "theory" often is used as a synonym for a hunch or guess. Consequently, people sometimes misinterpret the phrase "evolutionary theory" to mean some kind of guess that lacks critical support. In scientific terminology, however, a theory is a well-developed integration of observations, experiments, and interpretations. Scientists use the word "hypothesis" to refer to a "possible explanation" that remains to be tested.

Reference:

Campbell, N.E. & Reece, J.B. (2002). *Biology*, (6th ed.). San Francisco: Benjamin Cummings.

Image Reference:

Wikimedia Commons. (2005). From: Pearson, K. (1859-1860). Charles Darwin. *The life, letters and labours of Francis Galton.* Retrieved 1-26-2006, from http://en.wikipedia.org/wiki/File:Charles_Darwin_aged_51.jpg.



Natural Selection

Darwin spent many years collecting evidence from different sources to support his theory that evolution occurs through the process of natural selection. He carefully studied specimens that he and others had gathered from around the world, including several different species of finches from the Galapagos Islands. Darwin recognized, for example, that the different types of beaks he observed among the finches were related to different food sources and foraging patterns. Finches that fed on large seeds, for example, had thicker, stockier beaks, which contrasted with the more pointed beaks of finches that fed on cactus.

Darwin proposed that natural selection could explain how diversity—such as the diverse forms of beaks in the Galapagos finches—arises in nature. He reasoned that when environmental conditions change (e.g., alterations in temperature or sources of food), some individuals will have characteristics that allow them to continue to survive in the changed environment. These "successful" individuals will be more likely to produce more offspring than other less successful, and perhaps less well adapted individuals. Over time, the useful adaptive traits would become more common in the population, and the detrimental traits would become increasingly rare. In the example of the finches, birds with thick, stocky beaks would have a foraging advantage if the most abundant food source consisted of large, hard-shelled seeds. Individual finches whose beaks were most suited to seed eating would, theoretically, be able to consume more food. Therefore, birds with thick stocky beaks generally would be healthier and produce more offspring than individuals with less effective beaks. Over time, the population would come to be predominated by the stocky beak type.

It is important to recognize that evolution by natural selection, which many people think of as "survival of the fittest," is not strictly based on physical attributes, but rather, on differential reproductive success of individuals within a population. In a biological sense, "fitness" is equivalent to success in producing offspring that also survive and reproduce.

Darwin had little understanding of the underlying genetic mechanisms that drove natural selection. He knew, however, that for this system to work, the offspring must inherit the parent's physical characteristics. Thus, the basic elements of natural selection are that: (1) variation is present; (2) variation is heritable; (3) individuals within a population have different reproductive successes; and (4) individuals with higher reproductive success leave disproportionately more offspring.

Reference:

Campbell, N.E. & Reece, J.B. (2002). *Biology* (6th ed.). San Francisco: Benjamin Cummings.

Image Reference:

Wikimedia Commons. (2006). From: Darwin, Charles. (1839). *The Voyage of the Beagle*. Retrieved 1-26-2006, from http://commons.wikimedia.org/wiki/File:Darwin%27s_finches.jpeg.

Domestication and Artificial Selection

Darwin used examples of artificial selection to help explain the process of natural selection. For thousands of years, humans have applied artificial selection to obtain domesticated plants and animals with desirable combinations of traits. Darwin noted how humans developed hundreds of dog breeds from one common ancestor (now known to be the wolf). Some dog breeds were developed for a particular purpose. For example, many of the characteristics of the dachshund breed of dogs–such as short legs, slender bodies, and courageous dispositions–were selected to develop individuals well suited to maneuvering through narrow holes while hunting badgers. Most plant and animal products we eat have been similarly modified through careful selection and breeding of individuals with desirable characteristics. For example, broccoli, brussels sprouts, cabbage and cauliflower all have been derived from the same common wild ancestor, a single species of wild mustard.

References:

Campbell, N.E. & Reece, J.B. (2002). *Biology*, (6th ed.). San Francisco: Benjamin Cummings.

Darwin, C. (1859). *The Origin of Species*.

Raven, P.H., Johnson, G.B., Losos, J.B., Singer, S.R. (2005). *Biology* (7th ed.). New York: McGraw-Hill.

Image Reference:

Wikimedia Commons. (2006). American Staffordshire Terrier (Ltshears). Retrieved 2-5-09, from http://commons.wikimedia.org/wiki/File:Amstafford.jpg.

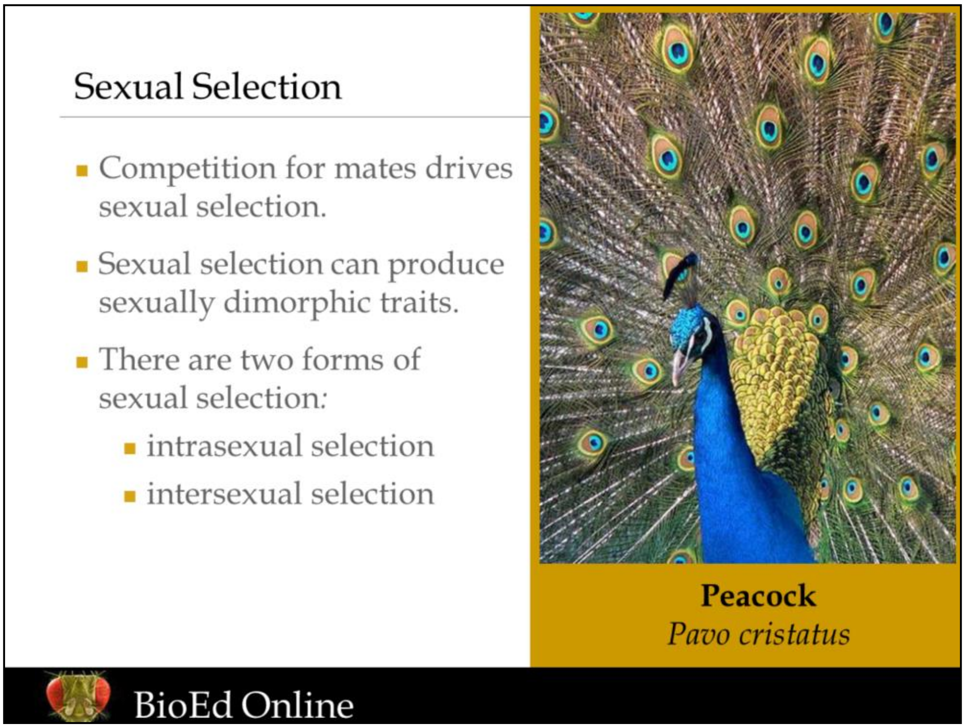
Wikimedia Commons. (2006). Bloodhound (Pleple2000). Retrieved 2-5-09, from http://commons.wikimedia.org/wiki/File:Bloodhund_r54.jpg.

Wikimedia Commons. (2005). Bichon frise (Sannse). Retrieved 2-5-09, from http://commons.wikimedia.org/wiki/File:Bichon_Frise_600.jpg.

Wikimedia Commons. (2006). Bulldog standing (Makemi). Retrieved 2-5-09, from http://commons.wikimedia.org/wiki/File:Bulldog_standing.JPG.

Wikimedia Commons. (2005). Chihuahua (L.M.B. Sanchez). Retrieved 2-5-09, from http://commons.wikimedia.org/wiki/File:Can047eue.jpg.

Wikimedia Commons. (2006). Miniature Dachshund (E.L. Finch). Retrieved 2-5-09, from http://commons.wikimedia.org/wiki/File:MiniDachshund1_wb.jpg.



Sexual Selection

Darwin expanded his principle of natural selection to explain sexually dimorphic traits (features that differ between the sexes), including why, for example, males of many species tend to have more showy traits, while females often are comparatively drab. Darwin proposed that competition for mating opportunities drives the process of sexual selection as long as the fitness benefits conferred by this selection outweigh the costs imposed by natural selection. For instance, elaborate male traits, such as the spectacular train (tail coverts) of the male peacock, are clearly important to attracting females during courtship. However, the large elongated train increases susceptibility to predators by reducing the males' flight capability. In contrast, peahens (female peacocks), for whom the males are competing, are relatively drab, and blend more successfully with their environments. Females are less vulnerable to predators, particularly during nesting season. Darwin noted that since females and non-breeding males lack exaggerated colors or displays, these features of breeding males probably are disadvantageous.

There are two basic forms of sexual selection: intrasexual and intersexual. Intrasexual selection is driven by direct competition among members of one sex. This can involve contests between males of a species to gain mating opportunities with females. Such male-male combat is found among deer, for example. Competition between males also may take place during reproduction. In some species, sperm from more than one male may compete to fertilize the female's eggs. In contrast, intersexual selection is driven by abilities of one sex to attract the attention of the opposite sex and be chosen as a mate. Females generally drive intersexual selection, as they choose males with which to mate based on "attractive" features, such as the showy courtship display of the peacock, or other features, such as size, vocalizations, or dominance of other males.

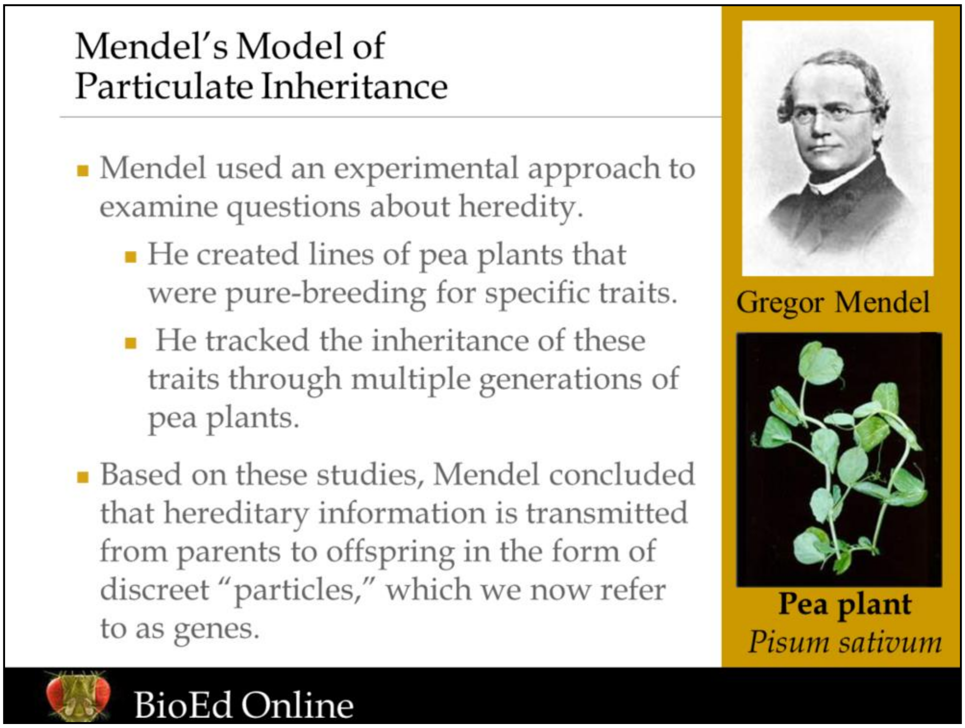
References:

Campbell, N.E. & Reece, J.B. (2002). *Biology* (6th ed.). San Francisco: Benjamin Cummings.

Darwin, C. (1871). *The Descent of Man and Selection in Relation to Sex.* Princeton Press.

Image Reference:

Wikimedia Commons. (2005). Peacock (*Pavo cristatus*), displaying his tail (B.S. Thurner Hof). Retrieved 2-4-08, from http://commons.wikimedia.org/wiki/File:Pfau_imponierend.jpg.



Mendel's Model of Particulate Inheritance

In contrast to Darwin's observational methods, Gregor Mendel used an experimental approach to examine questions about heredity. Interested in the fundamental question of how traits are passed from one generation to the next, Mendel spent eight years tracking the inheritance of specific traits through multiple generations of garden pea plants (*Pisum sativum),* in a series of studies that involved more than 28,000 plants.

For his studies, Mendel took advantage of the fact that pea plants are easy to breed and have distinctive and observable physical traits (phenotypes), including height, pea color and pea texture. He established pure breeding lines for these, and other phenotypes. These pure breeding lines are known as the parental, or P lines. As first steps in his experiments, Mendel crossed two different P lines, for example, plants with green peas and plants with yellow peas. He found that all of the offspring (known as the first filial, or F_1 line) looked like only one of the parental lines; they all produced yellow peas. The green pea trait of the second parental line had disappeared.

As the next step, he crossed the yellow-pea offspring (the F_1 line) produced by his original cross. The offspring produced by this cross (known as the second filial, or F_2 line) had a combination of phenotypes: ¾ of the F_2 offspring looked exactly like the previous F_1 generation; they had yellow peas. However, the remaining ¼ of the F_2 progeny displayed the green-pea trait of the original, parental line, which had been lost in the F_1 generation. Thus, variation was restored. Based on the results of his experiments, Mendel proposed that parents pass on discreet particles, or factors (what we now call genes), to their offspring.

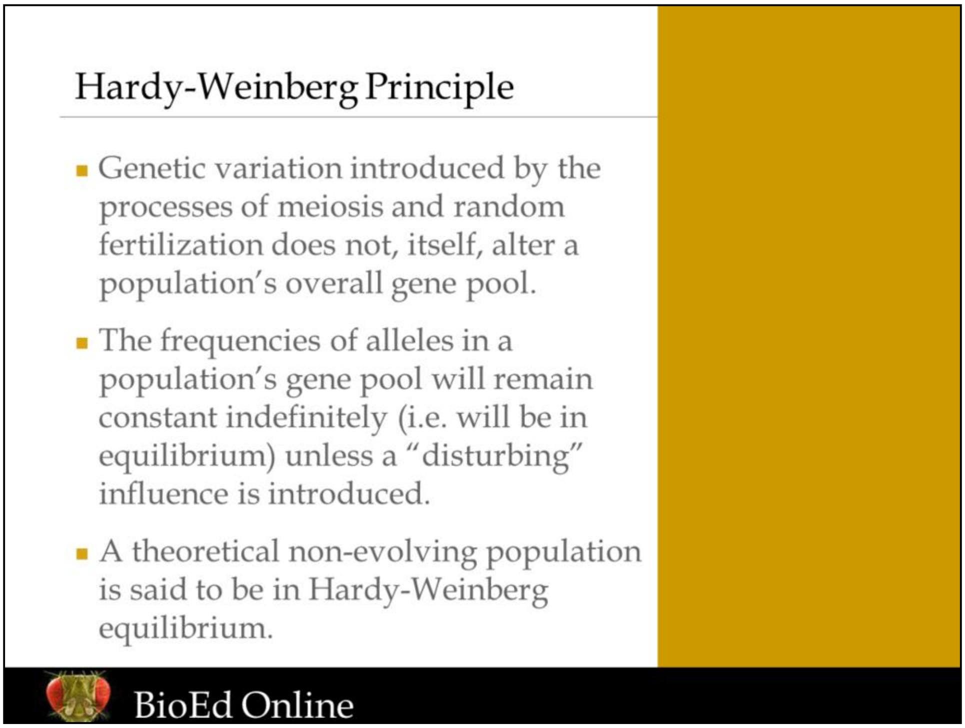
To learn more about Mendel's work, review the *BioEd Online* presentation entitled "Introduction to Mendelian Genetics."

Reference:
Campbell, N.E. & Reece, J.B. (2002). *Biology* (6th ed.). San Francisco: Benjamin Cummings.

Image References:

Wikipedia. (2006). Gregor Mendel. Retrieved 1-26-2007, from http://en.wikipedia.org/wiki/File:Gregor_Mendel.png.

Department of Primary Industries. (1997). *Image of Pea shoots (pisum sativum).* Institute for Horticultural Development (Permission granted 5-03-2005). Retrieved 4-20-2005 from http://www.dpi.vic.gov.au/trade/asiaveg/thes-48.htm



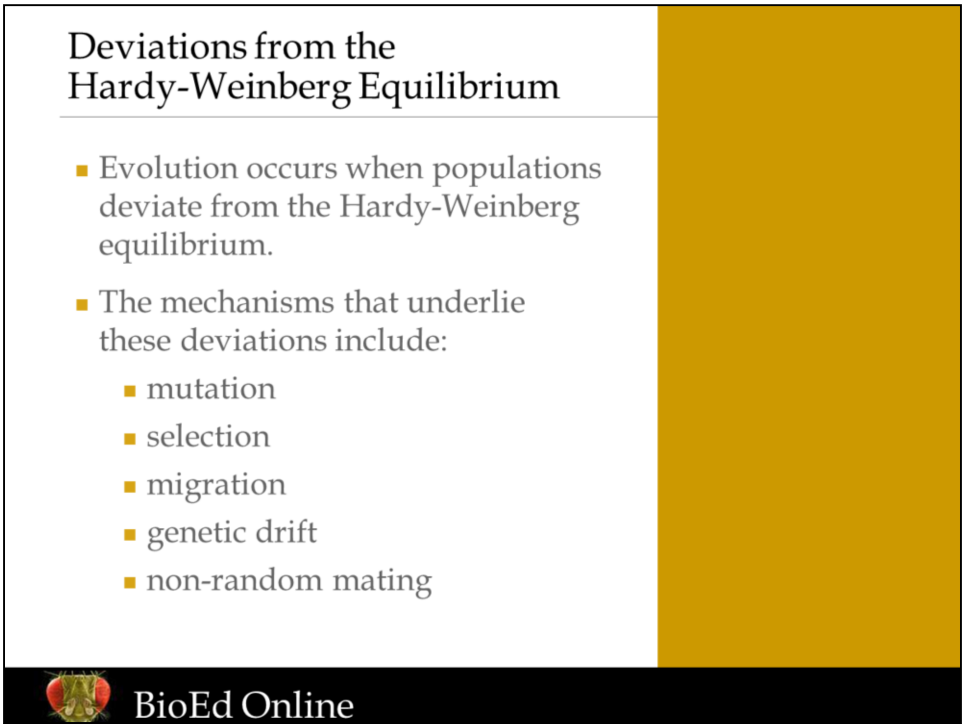
Hardy-Weinberg Principle

Early in the 20th century, the mathematician G.H. Hardy and the physician Wilhelm Weinberg, independently developed probabilistic models of genetic variation at the population level. The **Hardy-Weinberg principle** states that the gene pool of a population will remain constant indefinitely (i.e., it will be in equilibrium) unless a "disturbing" influence is introduced. In other words, the genetic variation introduced through the processes of meiosis and random fertilization does not affect a population's overall gene pool.

A theoretical non-evolving population is said to be in Hardy-Weinberg equilibrium. For a population to reach and maintain this equilibrium, it must meet specific criteria: it must be infinitely large, exhibit random mating patterns, have a constant, unchanging gene pool (no net mutation), have no migration into or out of the population, and have no natural or sexual selection occurring within the population.

Reference:

Campbell, N.E. & Reece, J.B. (2002). *Biology*, (6th ed.). San Francisco: Benjamin Cummings.

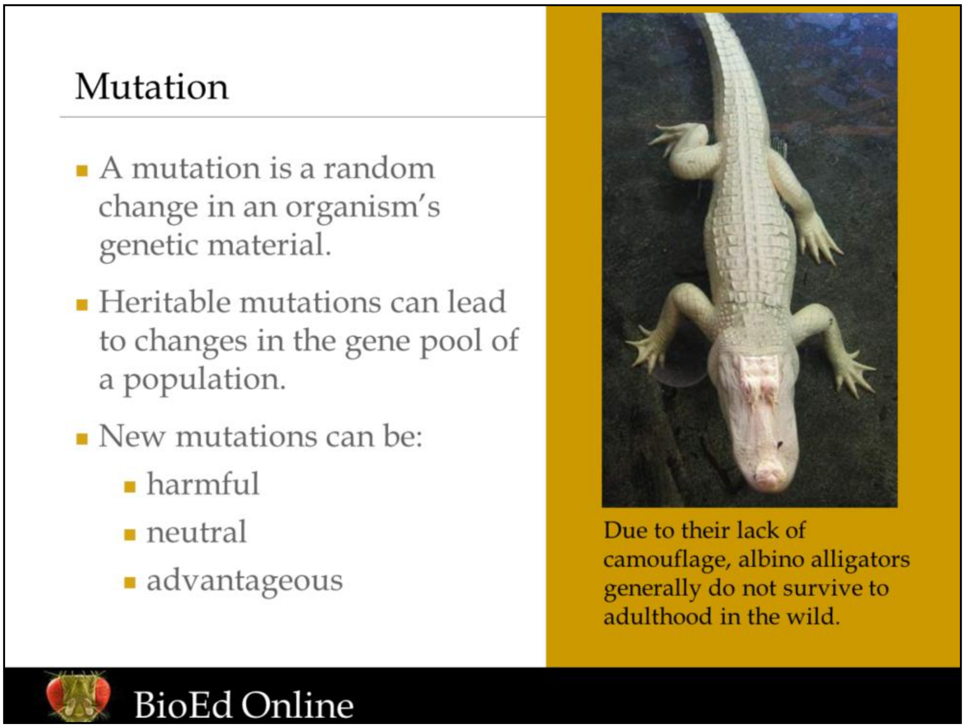


Deviations from the Hardy-Weinberg Equilibrium

Hardy-Weinberg calculations identify the allelic and genotypic frequencies expected from generation to generation, when a population is in Hardy-Weinberg equilibrium. For a population to reach and maintain this equilibrium, it must meet criteria (e.g. random mating patterns, no mutation, no selection) that are essentially unattainable outside of a laboratory setting. Thus, evolution occurs when natural populations deviate from Hardy-Weinberg equilibrium, causing shifts from the expected allelic and genotypic distributions. The major mechanisms that drive these shifts are selection, mutation, migration, genetic drift, and non-random mating.

Reference:

Campbell, N.E. & Reece, J.B. (2002). *Biology* (6th ed.). San Francisco: Benjamin Cummings.



Mutation

Remember that genetic variation contributes to the evolutionary potential of a population. A mutation, or a random change in an organism's genetic material, can lead to changes in the gene pool if the mutation is heritable (carried by the sperm or eggs). The word "mutation" also refers to the process by which a gene or chromosome is modified. Although they are relatively rare occurrences, mutations can introduce new alleles into a population and, therefore, provide raw material for the evolutionary process.

Because mutation is a random event, new mutations can be either harmful, neutral, or advantageous. Harmful mutations, like the albino alligator depicted in the figure, confer lower fitness (reproductive success) to an individual. Neutral mutations have no net effect on the fitness of an individual. Advantageous mutations increase fitness, providing an advantage to an individual. The frequency of an allele that confers a fitness advantage is likely to increase in a population.

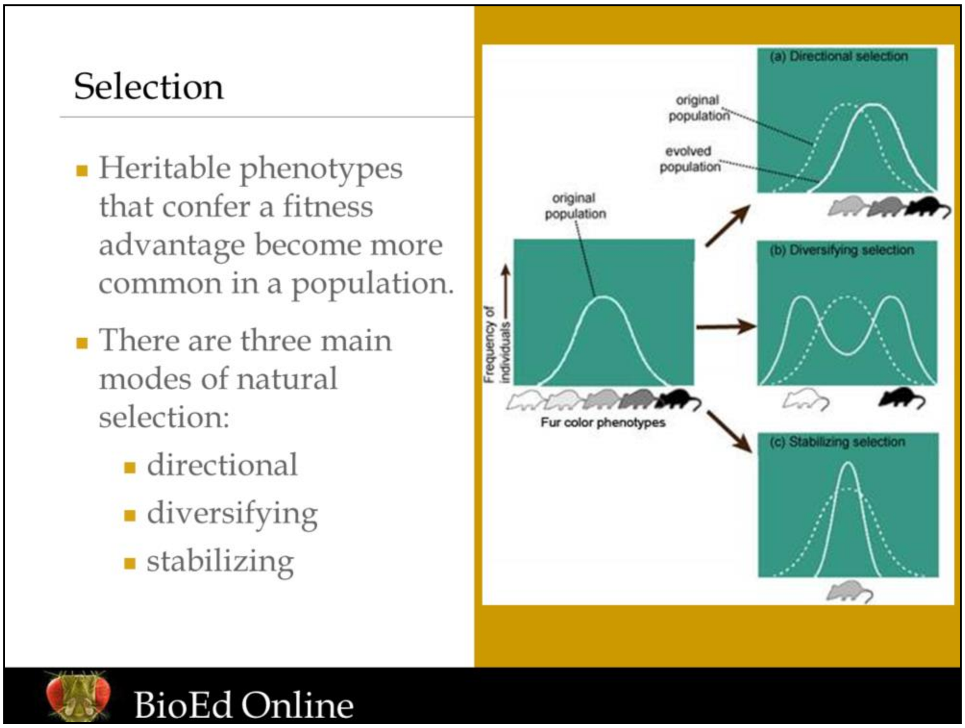
Mutations only have evolutionary consequences if they are passed on to the next generation. Examples of types of mutations include changes in DNA sequence at specific locations (point mutations), sequence changes as a result of recombination, and changes caused by transposable elements (copies of DNA sequences that become inserted into different sites in the genome).

Reference:

Campbell, N.E. & Reece, J.B. (2002). *Biology*, (6th ed.). San Francisco: Benjamin Cummings.

Image Reference:

Wikimedia Commons. (2007). Albino alligator (Jon Zander). Retrieved 2-3-09, from http://commons.wikimedia.org/wiki/File:Albino_Alligator_2.JPG.



Natural Selection

Selection is one way that genetic shifts in populations (evolution) occur. Through natural selection, traits (and the alleles that confer those traits) that are beneficial to reproductive success become more common in a population, while those that are detrimental become increasingly rare. There are three main modes of natural selection: directional, diversifying, and stabilizing.

In directional selection, individuals with one extreme phenotype exhibit an advantage in fitness (reproductive success) over the others. In time, the mean (average) of the population shifts toward that extreme phenotype (see figure “a”). For example, if dark fur helped mice absorb heat from the sunshine on a cold winter day, and thereby gave them a survival advantage, a disproportionate number of their dark fur alleles would be passed on from generation to generation. The mean coat color of the population would shift to darker and darker values over time, thereby increasing the proportion of individuals with good warming features.

Under diversifying selection, individuals with extreme phenotypes at either end of the spectrum (the lightest and darkest coats in this example) have higher fitness than those with the average phenotype, and thereby pass on a larger number of alleles to descendent generations. Through time, the distribution of the phenotype within the population changes such that most individuals exhibit one of the extreme phenotypes. Figure “b” illustrates this process. Mice with the darkest or lightest coats have higher fitness than those with medium coat colors, and therefore, become more common in the population.

In stabilizing selection, individuals with the average phenotype have higher fitness than those with the extreme phenotypes. In this scenario, the range of phenotypes decreases over time (see Figure “c”). Mice with average coat color have higher reproductive success, perhaps because their plain fur helps them hide them from predators. Their fitness results in a disproportionate number of alleles for the average coat color being passed on to future generations. In contrast, mice carrying alleles for extreme coat colors eventually would be weeded out because, in this example, they are easier targets for predators and thus, less likely to reproduce.

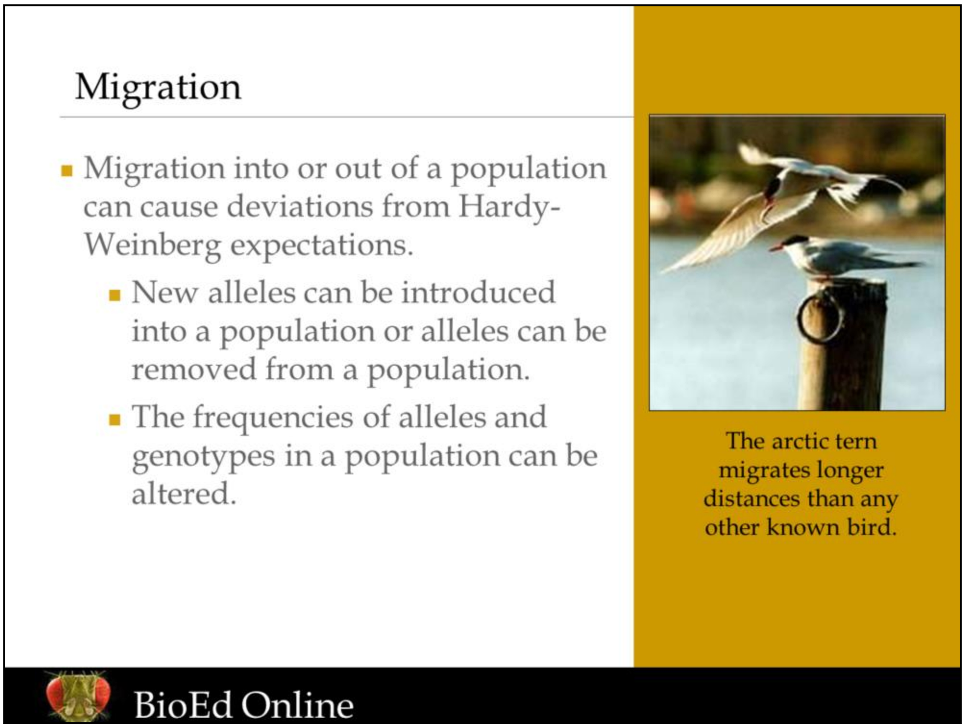
Populations under selection pressures will have changes in allelic frequencies and will, therefore, deviate from Hardy-Weinberg expectations.

Reference:

Campbell, N.E. & Reece, J.B. (2002). *Biology* (6th ed.). San Francisco: Benjamin Cummings.

Image Reference:

Baylor College of Medicine. (2009). Center for Educational Outreach. Houston, TX: Baylor College of Medicine. Adapted from: Campbell, N.E. & Reece, J.B. (2002). Figure 23.12. *Biology* (6th ed.). San Francisco: Benjamin Cummings.



Migration

Migration, or the geographical movement of organisms, can cause deviations from Hardy-Weinberg expectations (and therefore can provide raw material for evolution) by changing the gene pools of different populations. Through migration, new alleles can be introduced or taken away from a population, or the frequencies of alleles and genotypes in a population can be altered.

Suppose that population **1** has only alleles “a” and “b,” while population **2** has only alleles “x” and “y.” If individuals from population **2** move into the same area as population **1** and breed with individuals from population **1**, they will introduce the “x” and “y” alleles.

Now suppose that all individuals from population **1** carrying the “a” allele migrate into the area containing population **2** and interbreed with that population. Population **1** (individuals that did not migrate into the area of population **2**) will undergo a decrease in genetic variation, because it is left only with individuals carrying the “b” allele. Meanwhile, population **2** will experience an increase in variation, because it has gained the “a” allele.

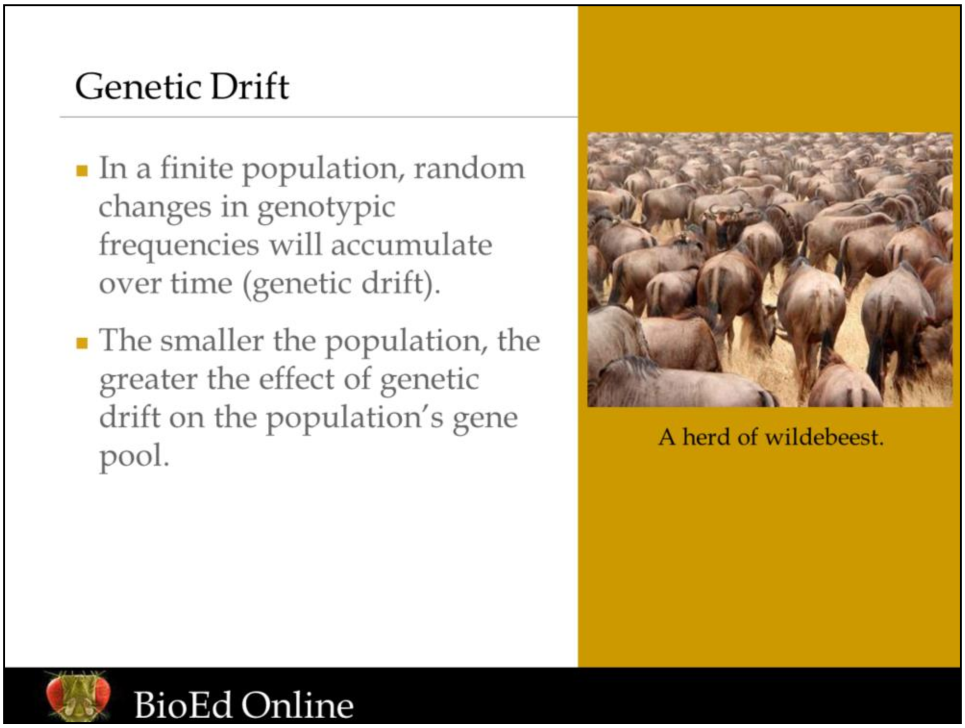
A more subtle way for migration to alter Hardy-Weinberg expectations is by shifting the relative frequencies of alleles, even when the number of alleles remains unchanged. Suppose population **3** also has only alleles “a” and “b.” And suppose the “a” allele is common in population **1,** but rare in population **3**. If population 1 migrates and interbreeds with population 3, allelic frequencies will change and the differences between the two populations will be reduced.

Reference:

Campbell, N.E. & Reece, J.B. (2002). *Biology*, (6th ed.). San Francisco: Benjamin Cummings.

Image Reference:

Wikimedia Commons. (2005). Arctic Terns (T. Toivanen and T. Toppila). Retrieved 02-02-2007 from http://commons.wikimedia.org/wiki/File:Arctic_terns.jpg.



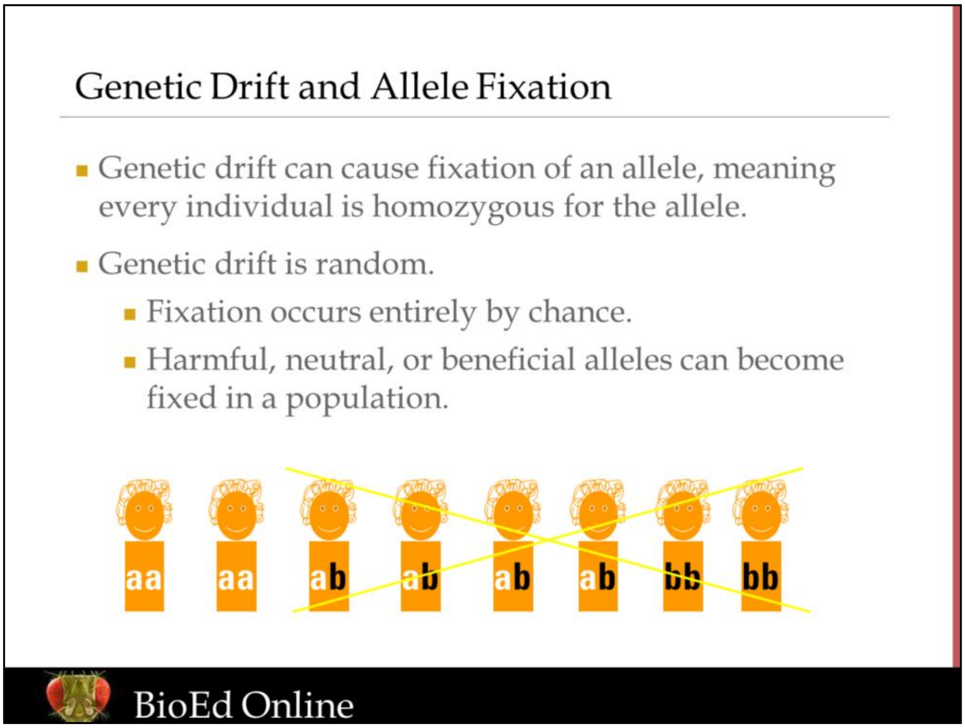
Genetic Drift

Most populations are limited in size, and many can be very small. In small populations, dramatic changes in allele frequency can occur simply by chance. This is an evolutionary mechanism called genetic drift. The smaller the population, the greater the effect of genetic drift on the population's gene pool. When only a random subset of individuals contribute to the next generation, the statistical properties of sampling cause random deviations in allele frequency and consequent genotypic frequency.

Reference:
Campbell, N.E. & Reece, J.B. (2002). *Biology*, (6th ed.). San Francisco: Benjamin Cummings.

Image Reference:

Wikimedia. (2007). The leading gnu (V.G. Pini). Retrieved 2-4-09, from http://commons.wikimedia.org/wiki/File:The_leading_gnu.JPG.



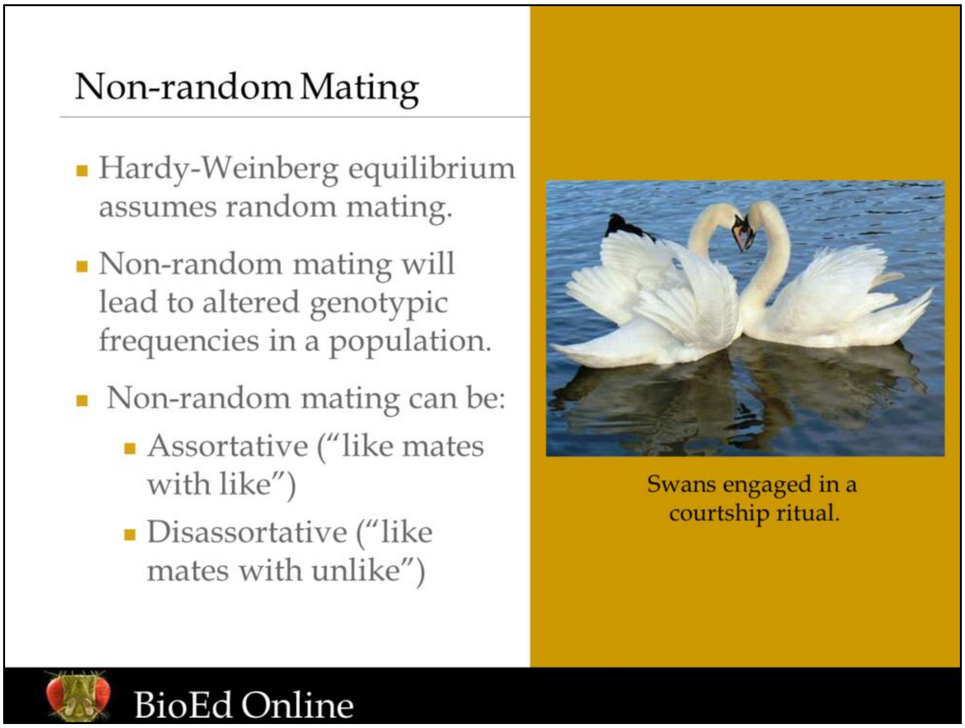
Genetic Drift and Fixation of an Allele

Imagine a small population with only two alleles, “a” and “b.” Then imagine that, by chance, a tree fell on a random set of individuals and that the survivors happened to be homozygous for “a.” Obviously, only the survivors will reproduce, so the “b” allele will no longer be present in future generations. In this case, the “a” allele is said to be fixed in the population. That is, every individual is homozygous for the “a” allele. This dramatic case illustrates fixation in a single generation. In large populations, genetic drift is more likely to alter the allelic (and genotypic) frequencies from one generation to the next. Through time, however, genetic drift can lead to fixation even in large populations.

Notice that in this example, the “a” allele became overrepresented entirely by chance: a tree fell and eliminated all members of the population carrying the “b” allele. As we have seen, evolutionary processes are not always adaptive (resulting from natural selection). Genetic drift can fix any allele, regardless of whether it is harmful, neutral, or advantageous. Suppose the homozygous “aa” individuals in our example had some disease that reduced their fecundity (number of offspring per mating), relative to individuals with at least one “b” allele. Natural selection would have favored an increase in the “b” allele, but the strong effects of genetic drift (from the effects of the falling tree) took over and fixed the disadvantageous allele within the population.

Reference:

Campbell, N.E. & Reece, J.B. (2002). *Biology*, (6th ed.). San Francisco: Benjamin Cummings.



Non-random Mating

Deviations from Hardy-Weinberg expectations of gene frequencies within a population also occur through non-random mating, which can lead to altered genotypic frequencies. In assortative mating, "like mates with like." In other words, individuals with similar phenotypes, and thus similar genotypes, are more likely to mate with each other than at random. Human populations are among those that exhibit assortative mating for a great number of features (genetic and non-genetic), such as height. Tall women are more likely to mate with tall men and short women are more likely to mate with short men. This kind of non-random mating violates the assumptions of Hardy-Weinberg equilibrium by creating an excess of homozygotes.

In disassortative mating, "like mates with unlike." That is, individuals with dissimilar phenotypes, and thus dissimilar genotypes, are more likely to mate with each other than at random. This kind of non-random mating violates the assumptions of Hardy-Weinberg by creating an excess of heterozygotes.

Reference:

Pawlowski, B. (2002.) Variable preferences for sexual dimorphism in height as a strategy for increasing the pool of potential partners in humans. *Proclamations Royal Society London*, 270, 709 -712.

Image Reference:

Wikimedia Commons. (2006). The Heart (mozzercork). Retrieved 2-4-09, from http://commons.wikimedia.org/wiki/File:Mozzercork_-_Heart_(by).jpg.

Summary: Evolutionary Theory

- Darwin's insights offered an explanation of how inherited variation arises in nature.
- Mendel provided a model of particulate inheritance.
- Probabilistic models developed by Hardy and Weinberg helped to merge and fill out Darwin's and Mendel's observations into what we call "The Modern Synthesis" of evolutionary theory.
- Evolution occurs when populations deviate from the gene frequencies expected in a population (Hardy-Weinberg equilibrium) as a result of mutation, selection, migration, genetic drift and/or non-random mating.