THE CAUSES OF EVOLUTION

OVERVIEW

The second of the two major fields of evolutionary biology is described in this section: microevolution. The overall goal of this field is to understand, in detail, the causes of evolution. First, the major causes of evolution are described, and then the most important cause of evolution is focused upon: natural selection.

EVOLUTION AND THE HARDY-WEINBERG PRINCIPLE

Evolution, in its most narrow definition, is a change in the genetic composition of a population from one generation to the next. As an example, let us say that in a particular population, there are two versions of a gene (i.e. two alleles) in some proportion (e.g. 0.45 & 0.55). In other words, 45% of the alleles in the population are “A” and 55% are “a.” If the proportion of alleles in a population changes from the parent generation to the offspring generation (e.g. from 0.45 & 0.55 ✍ 0.35 & 0.65), the population is said to have evolved. This is known as the population genetic definition of evolution, and it can be applied to one gene or to a combination of many genes.

There are several key points here:

- ***populations** evolve, not individuals*
  - individuals do change throughout their lives, sometimes quite dramatically (e.g. butterfly life cycle), but this is not evolution
- ***evolution is a change in the genetic composition of a population***
  - variation in a population that is due to non-genetic (i.e. environmental) causes does not evolve
- ***evolution occurs across generations***

The Hardy-Weinberg Principle is a useful tool for understanding the causes of evolution. If the assumptions of H-W hold in a particular population, then the H-W principle tells us that after one generation of random mating, the population will be at equilibrium (i.e. the population will not change). In other words, *the H-W principle tells us what to expect if a population is* <u>*not*</u> *evolving*. If any of the assumptions are violated, then allele frequencies may change (i.e. the population may evolve). Investigation of the assumptions of H-W can help us to identify the causes of evolution.

THE CAUSES OF EVOLUTION

The following are the five assumptions of the Hardy-Weinberg Equilibrium:

1) **random mating** within the population
2) **no mutation**
3) **no gene flow** (population is isolated from other populations)
4) **infinite population size**
5) **no differential reproductive success**

In the following discussion, we will investigate each of these assumptions. Specifically, we will ask, if the assumption is violated, does a change in allele frequency occur? *If a violation of the assumption does change allele frequency, then it is a cause of evolution*.

Assumption 1: Random mating

If mating within a population is not random, it is said to be non-random. There are many examples of non-random mating. For example, individuals are more likely to breed with other individuals that are close by, than they are with individuals that are very far away.

Let us take an extreme example of non-random mating (complete inbreeding by self-fertilization in plants) to investigate whether it is a cause of evolution. When a plant pollinates its own ovules with its own pollen, it is said to have self-fertilized (or "selfed"). This is non-random in that the plant does not mate randomly with any individual, but rather only with itself. In a population of individuals all heterozygous at some gene (A/a), if all the individuals self, what will be the genetic composition of the next generation? Here are the results of a self-fertilization cross (the progeny from an individual self-fertilizing), and the resulting population allelic frequency in the next generation. Here and throughout this section, "p" refers to the proportion, or frequency of the “A” allele in a population, while “q” refers to the frequency of the “a” allele:

Results of a Cross by Self-fertilization:

Generation 1		Generation 2
Aa x Aa	✍	1 AA : 2 Aa : 1 aa

Resulting Population Allele Frequencies:

Generation	p	q
1	0.5	0.5
2	0.5	0.5

Genotypic frequencies do change from one generation to the next (from all Aa to a ratio of 1 AA : 2 Aa : 1 aa). However, allele frequencies do not change (p = q = 0.5). ***Nonrandom mating, by itself*[1]*, is not a cause of evolution*** (defined as change in allele frequencies); however, it does change the genetic composition (genotypic frequencies) of the population.

Assumption 2: No Mutation

Mutation can change allele frequencies. As an example, let us start with a population of 50 individuals that are homozygous for a gene (all 50 individuals are AA). If a mutation (A ✍ a) occurs in a gamete of one of these individuals, and that gamete is passed on to the next generation, then the genetic composition of the population has changed across generations:

Generation	p	q
1	1.0	0
2	0.99	0.01

Mutation is a cause of evolution. However, mutation is a rare event, and therefore does not greatly affect allele frequencies. It is a cause of evolution, but it is not a very important cause of evolution. ***The importance of mutation to evolution is not as a cause of evolution, but as a mechanism of producing genetic variation within populations***.

[1] Non-random mating, in conjunction with another cause of evolution (e.g. selection) can be very important to the evolution of a trait. For example, If a female bird chooses to mate only with males that have long tails, this is non-random mating; however, the female preference is a form of selection, called sexual selection.

Assumption 3: No Gene flow

Gene flow is a cause of evolution. Gene flow (also called **migration**[2]) is the movement of alleles from one population to another. Alleles are moved between populations when animals disperse to new locations, and when pollen and seeds are blown by wind or moved by water or animals. As an example, let us say that all the individuals on an island are homozygous for "a" (aa), while all of the individuals on a continent are homozygous for "A" (AA). Gene flow between these two populations will change the allele frequencies of both populations:

	Island		**Continent**	
Generation	p	q	p	q
1	0	1.0	1.0	0
2	>0	<1.0	<1.0	>0

Assumption 4: Infinite population size

When populations are finite, sampling errors will occur from one generation to the next. As an example, we will start with a finite population of ten individuals with the genotypes: 3 AA, 4 Aa, 3 aa, thus with allele frequencies of p = q = 0.5. If all other assumptions of H-W hold (i.e. random mating, no differential reproductive success, etc.) then what will be the allele frequencies in the next generation? If you simulate this process with a coin toss (using a fair coin that has an equal probability of getting a "heads" or a "tails") and designate a heads toss as a "A" allele and a tails toss as a "a" allele. Flip a coin to determine the genotypes of individuals in the next generation (i.e. random mating). With the first two tosses, if you get (heads, heads) this individual is AA; if you get (heads, tails) or (tails, heads), this individual is Aa; if you get (tails, tails) this individual is aa. Continue until you have a population of ten individuals, then calculate the allele frequencies. If you do this a hundred times, then some of the time, you will get p = 0.5 in the next generation. However, there is also a probability that you could get p = 0.4, p = 0.6, p

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[2] Technically, **migration** is a pattern of seasonal movement of an animal, such as when birds migrate south for the winter. This is not the same as gene flow, which is when an animal disperses from its natal population to a different population, and breeds there. This is more appropriately called "dispersal."

= 0.3, p = 0.7, etc. In fact, there is some probability of getting any allele frequency from p = 0 to p = 1.0.

Evolution caused by sampling error is called **genetic drift** (or random genetic drift), which are random changes in allele frequency in a population due to the unpredictability of sampling. ***Genetic drift is a cause of evolution***. Since no population is infinite, ***genetic drift occurs in every population.*** But the effects of genetic drift vary depending on the size of the population. *Small populations are more subject to the effects of drift than are large populations*. This is because, the smaller the sample, the greater the chance of deviation from the expected frequency (of no change from one generation to the next). Convince yourself of the effect of genetic drift on population size by doing the following exercise (methods as described in the previous paragraph): start with a population of 5 individuals (p= 0.5); simulate random mating by flipping a coin 10 times to get the next generation of individuals; calculate p for the next generation. Then, do this same experiment with different sized populations (e.g. 5 individuals, 10 individuals, 20 individuals).

Genetic drift can be an important cause of evolution, particularly in small populations that have recently colonized a new area. The **founder effect** occurs because the particular individuals that happen to “found” a new population are unlikely to be a fair genetic representation of the original population. Some alleles will be over-represented, some alleles will be under-represented, and some alleles will not be represented at all (lost).

There are many examples of the founder effect in humans. For instance, the Pennsylvania Amish have descended from a population of only about 200 individuals. One of these founding individuals happened to have Ellis-van Crevald syndrome, which is a rare type of dwarfism caused by a single gene. In most populations, the frequency of the allele for this rare syndrome is: q = 0.001; in the current Pennsylvania Amish population, the frequency is: q = 0.07. This rare syndrome is much more common in the Pennsylvania Amish (70 times as common), because one of the founding members of the population happened to have the allele that causes the syndrome.

Assumption 5: No Differential Reproductive Success

The Hardy-Weinberg Principle assumes that there is no differential reproductive success. In other words, every individual with a certain character state leaves the same number of offspring as other individuals with a different character state. When there is no differential reproductive success (along with the other assumptions of H-W) then evolution does not occur. However, when individuals with different characteristics differ in the number of offspring they produce, evolution does occur. This is called **natural selection**.

A famous example of natural selection is industrial melanism. Industrial melanism has been found in more than 70 moth species, but the best studied is *Biston betularia*, the peppered moth. Before the industrial revolution, most of the individuals in *B. betularia* populations were the peppered form (speckled white in color), while only a few were melanic (dark black in color). After the industrial revolution polluted the air and the lichen living on the trunks of trees died, the melanic form increased to greater than 90%. In unpolluted areas, the peppered form remained predominant.

{{insert photograph of moths}}

Experiments showed that the peppered moths were camouflaged from bird predators on lichen-covered (unpolluted) trees, while melanics were camouflaged on polluted, dark trees. Prior to human-caused pollution, individuals with the peppered form survived the best—they blended with the lichen, and birds could not find them as readily as they could find individuals that were melanic, which could easily be seen on the lichen. After smog and soot killed the lichen and the dark tree bark was exposed, the situation changed. Areas with lots of industry had dark trees, and now the peppered individuals stood out. This suggested that selection by birds decreased the survivorship of peppered moths on polluted trees. In other words, more peppered moths were killed and therefore left fewer offspring than melanic moths. Since moth coloration has a simple genetic basis, when the population changed from mostly peppered to mostly melanic, the population also changed allele frequencies (from mostly the peppered allele to mostly the melanic allele). *The population had evolved.*

The above example is of selection on a discretely varying character: moths are either peppered or melanic, and this character is determined by variation at one gene. The following is an example of natural selection acting on a continuously varying character, bill size in Darwin's finches, which has a very strong genetic basis (heritability of 0.9, which basically means that

90% of the variation in the population can be attributed to variation in genes, rather than environment).

{{insert photograph of finches}}

Peter and Rosemary Grant have conducted a long-term study on Darwin's finches (*Geospiza fortis*) on the Galapagos Islands. During 1977, there was a severe drought that changed the relative proportion of seeds on the islands: after the drought, there were far fewer small seeds, and many more large seeds. Previous work on the finches showed that larger-billed birds feed more efficiently on large seeds, while smaller-billed birds do better with small seeds. During the year of the drought, the Grants observed the fate of every bird on the island (several hundred individually marked individuals) and they noted that birds with smaller beaks starved to death, while those with bigger beaks survived. In the following year, 1978, the Grants returned to the island and measured the bill sizes of the surviving population, and found that the survivors' bills were significantly larger than those in the previous population (during 1976, before the drought). Natural selection had favored the birds with larger bills, because they could feed more efficiently on larger seeds, which were the majority of seeds left after the drought. This led to a measurable genetic change in the population: more large-billed birds. *The population had evolved.* ***Natural selection was the cause of evolution*** in both of these examples.

NATURAL SELECTION

What is natural selection?

Natural selection is defined as differential reproductive success among phenotypes. In other words, natural selection occurs when there is variation in some trait in a population, and individuals with one particular character state leave more offspring than individuals with other character states. In the moth example, this would mean that after the industrial revolution, individuals that were melanic produced more offspring than individuals that were peppered.

Natural selection can cause evolutionary change in a population if the phenotypes also differ in their genotypes (i.e. the variation in the character has a genetic basis).

Differential reproductive success can be quantitatively estimated by measuring the average **fitness** of individuals with different genotypes. *Fitness is made up of two components:* ***survivorship*** (to reproduction) *and* ***fecundity*** (i.e. number of offspring produced). If two genotypes differ in fitness, then natural selection is occurring.

Fitness is not a static character of an organism: ***fitness depends on the current environment***. For example, in the industrial melanism example, which color morph is favored depends on the environment. In unpolluted areas, the trees are covered with lichen, and the peppered genotype is favored as it is camouflaged from birds on these trees. In polluted areas, the lichen dies, and the trees are darker in color, which favors the melanic genotype (which is more camouflaged on these trees).

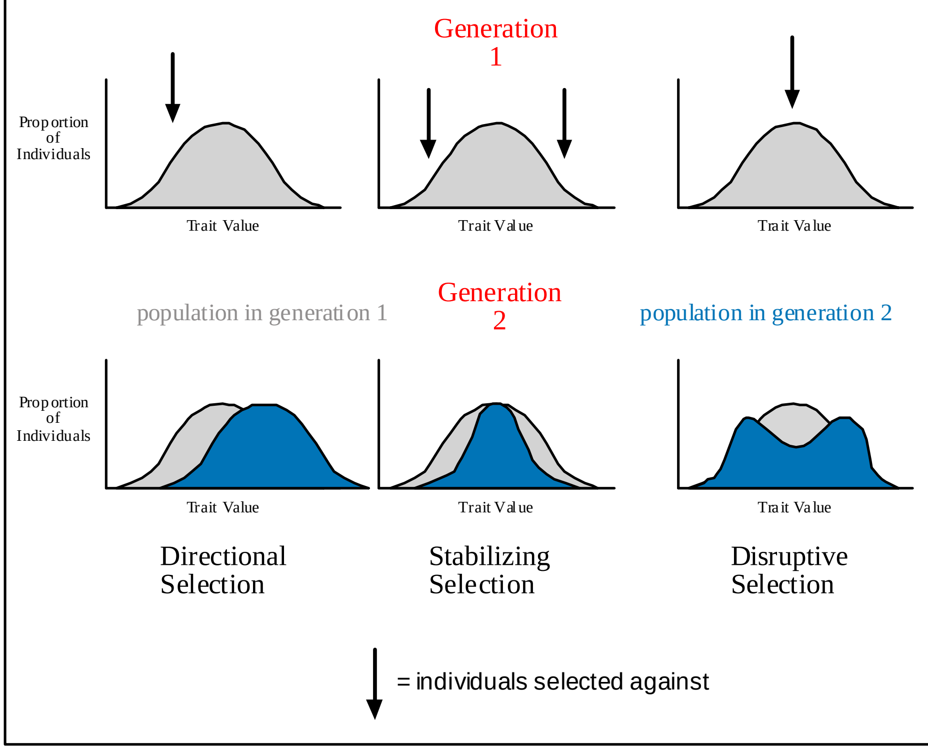
Natural selection occurs when a biological or environmental factor acts as an **agent of selection** on variation in some trait. In the industrial melanism example, the agent of selection on moth coloration is most likely bird predators. Birds are visually searching predators, so they select the moths they are able to find. The peppered moths are harder to see on the lichen-covered trees, and are therefore not taken as often as the melanic moths. However, when the peppered moths are on polluted, dark trees, they are easier to see than the melanics, and are therefore eaten more often. The agent of selection on bill size in the Darwin's finches was the size of the available seeds.

How does natural selection affect the evolution of traits?

There are three basic ways that natural selection can affect a trait (also called the three **modes of selection**): directional, stabilizing and disruptive (see Figure 1). ***Directional selection occurs when one extreme form of the character is favored.*** This form of selection is very common in changing environments. Industrial melanism is an example of a discretely varying character under directional selection. Bill size in Darwin's finches is an example of a continuously varying character under directional selection (for large bills).

Stabilizing (or balancing) selection occurs when an intermediate form of the character is favored, while extreme forms of the character are selected against. This type of selection is thought to be common in nature, especially in relatively stable/unchanging environments, as it is selection for "maintaining the status quo." Selection acts against any change in the character. An example of this type of selection on a discretely varying character is sickle cell anemia in humans. This disease is caused by a single gene that has two alleles (A/S). Individuals homozygous for the S allele at this gene have red blood cells that are sickle in shape. SS Individuals usually die very young. Individuals homozygous for the A allele (AA) have normal red blood cells. Individuals that are heterozygous (AS) have red blood cells that under normal conditions do not sickle. However, they do sickle when they are exposed to low oxygen levels.

Figure 1: Modes of Selection



The relative fitnesses of these three genotypes depend on the environment. Individuals that are SS are always selected against. However, in areas of Africa, the S allele is actually quite common. Why is that? It turns out that individuals that are heterozygous (AS) are resistant to malaria, a major killer in these areas. When the malaria parasite enters the red blood cells, the oxygen levels of the cells decrease, which causes them to sickle. When the red blood cell sickles, it kills the parasite, thus conferring resistance to malaria. Therefore, in Africa, where malaria is common, heterozygous individuals are favored over the two homozygous types: they do not have the full blown disease of sickle cell anemia (like SS individuals), and they are resistant to malaria (which AA individuals are not). Balancing selection at a single gene is also called heterozygous advantage.

The third mode of selection is ***disruptive (or diversifying) selection, which occurs when both extremes are favored over intermediates***. This form of selection may be important in speciation. One example of this type of selection is in beetle species with horned males. Often, within a single population some males have large horns, while other males have no horns at all. It turns out that males with large horns guard the tunnels in which female beetles lay their eggs. These guarding males are able to mate with the females, while keeping other males away. Males without horns, on the other hand, dig side tunnels and sneak into the main tunnels. By sneaking into tunnels, they bypass the guarding males and are able to mate with females. Males with intermediate-sized horns are not as good at guarding tunnels as the males with horns, and they are not as good at sneaking as the males without horns. In this case, selection favors individuals with large-horns and individuals with no horns (the two extremes), while individuals with intermediate-sized horns are selected against (they do not get as many mates).

{{insert photograph of horned beetles}}

ADAPTATIONS

Natural selection is the only mechanism of evolution that produces adaptations. Since the term adaptation has two very different uses in biology, it is worth making these definitions explicit. Both have to do with changes caused by an environmental change, but the mechanisms of the two are quite different. ***Adaptation, as used by physiologists, indicates an <u>individual's phenotypic</u> adjustment to a changing environment***. Another term for this is **acclimation**. An example of this would be when you travel to a very high altitude, at first your body is not used to the low oxygen environment, but after a few days, your body adjusts its chemistry to the low oxygen environment. Likewise, if you grow genetic clones of the same plant in two different environments (one very sunny and one very shady) the two clones will each adjust their phenotype during development to their environment. The shade plant will end up having longer internodes and broader leaves than the sun plant. Acclimation occurs within the lifetime of a single individual.

Adaptation, as used by evolutionary biologists, refers to a trait in a population that has evolved due to natural selection for some function. In other words, ***an evolutionary adaptation is a <u>population's genetic</u> adjustment to a changing environment***. In this case, the response to the environment occurs across generations. A few of the countless examples of genetic adaptations include: leaves that have been reduced to spines in cacti, moth wings that look like fallen dried leaves, vertebrate eyes, mollusk eyes, and insects' compound eyes, the very fast running speed of cheetahs, and even the ability to physiologically adapt (acclimate) to an unpredictable environment are all genetic adaptations.

Resource List

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McComas, W.F. 1994. Investigating Evolutionary Biology in the Laboratory. NABT

NAS, 1998. Teaching about Evolution and the Nature of Science. National Academy Press, Washington, D.C.

Ridley, M. 1993. Evolution. Blackwell Scientific Publications, Boston.

LESSONS ABOUT THE CAUSES OF EVOLUTION

There are many available lessons on natural selection and adaptation. Here, I separate them into two categories: simulations of natural selection, and "other" lessons on natural selection and adaptation.

CLASSROOM SIMULATIONS OF NATURAL SELECTION

There are two basic types of simulation lessons: single-generation and multi-generation. The nice thing about the single-generation lessons is they are quick and simple, but they run the risk of oversimplification. "**The Birds and the Beaks**" (McComas 1994) [[link to references cited page—see bottom]] is a very simple exercise using assorted tools and different sized beans (this is more of an exercise on adaptation, rather than natural selection). The Evolution and the Nature of Science Institutes (ENSI) has a nice single-generation exercise: "**The Natural Selection of Stick-Worms**," in which the students simulate birds feeding on different colored toothpicks [[www.indiana.edu/~ensiweb/lessons/ns.st.wm.html]]

There are many different multi-generation simulations to choose from. They each emphasize different types of natural selection, and use different materials. Which you choose will depend on what materials you have available, or what interests you the most, but it is worth checking out several so that you can pick and choose among them for specific methods, discussion questions, *etc.* ENSI has two: "**The Natural Selection of Bean Hunters**," which uses various implements to select colored beans [[www.indiana.edu/~ensiweb/lessons/ns.beans.html]] and "**The Chips are Down: a Natural Selection Simulation**," which uses colored paper chips on patterned backgrounds. [[www.indiana.edu/~ensiweb/lessons/ns.chips.html]] These both simulate selection by predators on some trait of their prey (selection for camouflage or mimicry of background coloration).

Access Excellence has two somewhat different simulations. "**Beans and Birds**" [[www.accessexcellence.org/AE/AEPC/WWC/1995/beansbirds.html]] is similar to the above lessons, except that the students must design their own experiment. "**Mimicry: an Example of Adaptation**" [[www.accessexcellence.org/AE/AEPC/WWC/1995/mimicry.html]] is different in that it uses the students themselves to simulate predators that learn to avoid distasteful food items, in order to discuss Batesian mimicry (in which a palatable form mimics the appearance of a distasteful form).

"**Investigating Natural Selection**" is a well-presented multi-generation lesson using fabric and paper chips. [[www.nap.edu/readingroom/books/evolution98/evol6-c.html]] Another one is "**Demonstrating the Effects of Selection**" (McComas 1994). [[link to references cited]] This is a very simple multi-generation simulation using two different colored beans to represent two alleles at a gene, with one allele dominant over the other. The recessive allele is lethal, leading to strong selection.

OTHER LESSONS ON NATURAL SELECTION

"**Evolutionstechnik**" [[www.indiana.edu/~ensiweb/lessons/origami.html]] is a simulation exercise of a different sort. The students build origami birds, and simulate random mutations and natural selection across generations. It also emphasizes incremental changes, divergence and many other evolutionary concepts. This is a fun exercise that emphasizes a lot of key concepts, but it takes a long time to do. To minimize class time, you may want to have materials ready and pre-cut, and possibly decrease the number of generations you simulate.

PBS' Evolution has a couple of lessons on natural selection in their Unit 4: How Does Evolution Work? [[www.pbs.org/wgbh/evolution/educators/teachstuds/unit4.html]] "**Darwin's Finches**" has the students examine the Grants' data on finch beak morphology both before and after a drought year, while "**Birds, Beaks, and Natural Selection—A Simulation**" is a simulation of bird beak evolution that is similar to the "Evolutionstechnik" exercise described above.

Tim Culp has developed lessons, "**Using Magnetobacteria to Study Natural Selection,**" which use magnetobacteria (north-seeking bacteria). A very simple form of this lesson can be found at Access Excellence. [[www.accessexcellence.org/AE/AEPC/WWC/1995/bacteria.html]] However, a more detailed lesson describing a nice experiment in which the students themselves actually exert selection for south-seeking bacteria can be found in The American Biology Teacher (Culp 1999).

The ENSI website has two other lessons on natural selection: "**What Darwin Never Saw,**" [[www.indiana.edu/~ensiweb/lessons/vid.wdns.html]] which uses a video of the same title that describes the work of Peter and Rosemary Grant on Darwin's finches in the Galapagos; and "**When Milk Makes You Sick,**" [[www.indiana.edu/~ensiweb/lessons/tp.milk3.html]] which is a lesson that applies evolution to medicine: what is the evolutionary explanation of lactose intolerance. This lesson is also available from Science Kit. The lesson as presented on the web is a bit confusing; the explanations are more user-friendly in the Science Kit packet.

MUSE (Modeling for Understanding in Science Education) has a very nice nine-week unit on natural selection. [[www.wcer.wisc.edu/ncisla/muse/naturalselection/index.html]] The focus of the unit is "the development, use, and extension of the natural selection model." Students learn the nature of scientific arguments, compare different explanatory models (Paley, Lamarck, and Darwin), and then use the natural selection model to explain several patterns in nature (e.g. monarch/viceroy mimicry). Even if you cannot spend a full nine weeks on a natural selection unit, it is still worth checking out this site to pick and choose among the various activities.

BioQuest Library VI [[www.bioquest.org]] is a collection of peer-reviewed computer simulations and databases. There are several modules that are relevant to evolution by natural selection, including: "**Evolve**," a simulation in which students can do various population genetic experiments on selection, genetic drift, *etc*; "**BGuILE: The Galapagos Finches**," a software application that depicts a drought episode on the Galapagos islands; "**BGuILE: TB Lab**," a simulated microbiology lab on antibiotic resistance in *Mycobacterium tuberculosis*; and "**BIRDD**," a database containing real data on the Galapagos finches, in which students can ask their own questions and collect relevant data. These applications are intended for use by undergraduate students, but may also be useful for high school students.

Also check out the PBS evolution video "**Learning and Teaching Evolution**," a companion to the series, [[www.pbs.org/wgbh/evolution/educators/teachstuds/svideos.html]] which contains short, seven-minute segments for use in the classroom. Segment four ("**How Does Evolution Really Work?**") gives a nice overview of the process of natural selection.

References Cited:

Culp, T. 1999. Demonstrating natural selection using magnetobacteria. The American Biology Teacher 61 (8): 616 – 620.

McComas, W.F. 1994. Investigating Evolutionary Biology in the Laboratory. National Association of Biology Teachers.