

The Theory of Natural Selection¹

Conservation Biology

Spring 2009

As we learned from our previous discussion, four factors change gene frequency in a population and so cause evolution. Two (mutation and migration) do so largely by introducing new alleles into the population. The other two (natural selection and genetic drift) do so by removing some alleles from the population while preserving others. Mutation, genetic drift and to some extent migration act in a random fashion and so produce chance deviation from the Hardy-Weinberg equilibrium. On the other hand, **natural selection (and sometimes migration) act in a non-random, directed fashion and produce adaptation.** For this reason natural selection is considered to be the centerpiece of modern evolutionary theory.

Both drift and natural selection require genetically based individual variation to effect evolution. What is the source of this variation in the population? **The ultimate source of all genetic variation is mutation,** but mutation does not occur frequently enough to be the major source of individual variation in any population. **The proximate (and by far the most common) source of the genetic variation** on which drift and natural selection act in any one generation **is sexual reproduction.** Whereas mutation by itself can add new alleles and slightly alter allelic frequencies, sexual reproduction cannot (see discussion of the Hardy-Weinberg law). That is not to say, however, that **sexual reproduction** is unimportant in evolution. It is extremely **important as the major supplier of individual variation.** Sexual reproduction, through Mendel's law of independent assortment and recombination, shuffles allelic variation (caused historically by past mutation) to produce the genotypic variation required by the theories of natural selection and genetic drift.

The Problem of Biological Variation

Due to independent assortment and recombination and the role of the environment, no two sexually reproducing individuals are exactly alike. The same can be said for populations and species. However, for a long time, especially when taxonomy was the most influential of the biological disciplines, individual variation was dismissed as unimportant. Taxonomists searched for characters shared by all individuals in a species that would define the species to which they all belonged. This idea of a **common essence** that defined a species (or any kind of object) was inherited from Plato and Aristotle who argued that the real world consisted of unseen perfect forms or **TYPES** which could be grasped by the intellect, and that the imperfect world revealed by the senses represented a mere shadow of the world of forms. **Variation was a nuisance** that clouded recognition of the perfect, immutable

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and eternal essence of each species. For these **typologists**, taxonomic characters shared by all individuals defined the species and these were unchangeable. **Because variation was ignored, the concept of evolution was unthinkable!**

Only when individual variation was recognized as important and populational thinking replaced typological thinking was the possibility of evolution taken seriously. Whereas **typological thinking** views all individuals in a population as being identical because they share a common essence or type, **populational thinking** views individuals as being variable so that a population exists as a range of individual variation characterized by an arithmetical mean and the spread around the mean (variance). **Without variation, there can be no change over time in a population and hence, no evolution.** The modern view of species defines them on the basis of reproductive compatibility, not on shared morphological characters and recognizes individual variation as the key to understanding how species might change over time.

Biological Variation and Evolution

The **statement that populations evolve – that they undergo genetic change over generations** -- is the statement of an inductive pattern. It, like the cell theory, is an inductive generalization rather than an explanatory theory. Evolution is evident to anyone who has looked, with an open mind, at biological variation over time, at the operation of heredity and at variation in the environment. It is as well established as any other scientific law. A variety of mechanisms to explain how evolution occurs have been suggested and each constitutes **a theory of evolution**. Modern evolutionary theory is a complex of those specific theories that have yet to be falsified by testing and therefore that contribute to our understanding of the varied processes behind evolution.

In the section below I am going to refer to **darwinism** when in fact the idea associated with this term (evolution by natural selection) was jointly announced by Darwin and Alfred Russell Wallace in 1859. Both should be remembered but the fact is that Darwin's work was of such quality and quantity that we refer to this idea as **darwinism**.

Darwinism

Darwin's great contribution was not the discovery of evolution; rather, he convinced a scientific community, already receptive to an evolutionary origin of organic diversity, that evolution and not special creation was the reason for the origin of species. In addition, he proposed a mechanism to explain the process behind evolution, namely, **his theory of natural selection**.

Darwin's proposed mechanism behind evolution follows logically from a series of **observations** and **deductions**:

1. **Organisms produce more offspring than can survive.**

Based on an amply documented **observation**.

2. **Adult population size remains constant from generation to generation.**

This is an **observation** that enjoys empirical support for some, but not all, species. However, those species whose population size fluctuates still do not increase or decrease indefinitely.

3. **There is a struggle for existence among offspring.**

This is a logical deduction or conclusion from the first two observations. If there only a fixed number of adults in each generation, and if more offspring are produced than are needed to replace them in the next generation, then it follows logically that many offspring will die in struggling to become the next generation's adults. Moreover, competition between individuals and their efforts to survive in given environments is amply documented.

4. **Individuals vary in their adaptation to (ability to survive in) the environment.**

This is an **observation** that has been carefully documented.

5. **These individual variations in adaptation are inherited**, i. e., they are under genetic control.

This **key point** was based on the **observation of the result of artificial selection and breeding experiments**. In 1859, it the weak point in his rationale because Darwin was unable to demonstrate the hereditary basis for individual variation. Darwin, therefore, had to **assume** that some heredity mechanism could explain how adaptive traits were passed on to offspring. We know Mendel was working at the same time but we believe that Darwin did not know of Mendel's work.

6. **On average those offspring with the better adaptations will survive.** "Survival of the fittest" as memorably summarized by **Spencer, not Darwin**.

This **deduction or conclusion** is derived from deduction #3 and observation #4, **but will only result in evolution if point #5 is true**.

Darwin and Wallace's Mechanism for Evolution: Is it a Theory?

Natural selection is neither a thing nor a theory. It is a process deduced from the rationale provided above. The reality of this process depends upon the empirical truth of these propositions and the logical integrity of the conclusions. If it could be demonstrated that propositions 1, 2, and 4 are not valid and/or not sufficient to deduce conclusions 3 and 6, then the process of

natural selection would not be an adequate description of how nature operates. **If proposition 5 is not true, then natural selection as a process will occur but will not result in evolution.** So far, however, these propositions have been empirically verified and seem logically sufficient to deduce the critical conclusions.

As is apparent from conclusion 6, Darwin viewed natural selection as a process of **differential mortality**; but **what really counts in evolution is reproduction, not survival**. No change will occur in a population in the next generation if some individuals outlive others, but do not reproduce. Darwin was well aware of this but used the term **sexual selection** for the evolution of traits that specifically contribute to the reproduce success of their possessors. Thus, *Darwin saw two forms of selection*:

(1) **Natural selection – a process that produces adaptations** by conferring a survival advantage on those individuals better able to resist predators, competitors or physical environmental forces, e.g., weather, and

(2) **Sexual selection – a process that did not produce adaptations in the strict sense of allowing individuals to survive in a given environment.** Instead, sexual selection is a process that acts to favor (reproductively) individuals:

- more attractive to the opposite sex (**intersexual selection**) or
- more successful in competing for mates with other members of their own sex (**intrasexual selection**).

Since what really matters in both forms is that the selected individuals leave more offspring than others in the population, **modern biologists define natural selection as a process of differential reproduction**. Sexual selection is seen as a process that is associated with better adaptation to a particular but very important part of the biotic environment – competition for mates. **Any phenotypic feature that increases ones ability to find mates is just as much of an adaptation as is the ability to obtain food or tolerate a particular temperature range.**

We will discuss the modern view of a mechanism that does not produce adaptation (nor does it produce maladaptation) in the next set of notes. This type of evolution is called **genetic drift**.

The Theory of Natural Selection

Darwin's theory of evolution by natural selection is not a statement of the reality of natural selection as a process; rather IT IS THE HYPOTHESIS THAT THE PROCESS OF NATURAL SELECTION CAUSES EVOLUTION, i.e., that it changes the genetic composition of a population between successive generations. Natural selection acts only within single populations (not between populations or species) and **the unit of natural**

selection (what is selected) **is the individual**. (Remember that on the other hand the unit of evolution is the population).

The result of natural selection is evolution, through the production of adaptation. **Adaptations are aspects of the phenotype that meet the needs imposed by the environment** and they are the result of gradual environmental selection of individual variants within a population. **To be selected, individuals need not be perfectly adapted to their environment - only better adapted than others in their population**. Thus, **natural selection results in directed evolution, not random changes in a species**. For this reason natural selection is considered to be the most important of all evolutionary forces (see Hardy-Weinberg's postulates - it is essentially a list of potential evolutionary forces).

As a process of differential reproduction (or mortality, as Darwin viewed it), natural selection is the choosing by an environmental agent of some individual variants over others for survival and reproduction. Hence, these chosen individuals produce the offspring that constitute the gene pool of the next generation. **This process, however, will not cause the gene pool to change between generations unless those individuals who are selected differ genetically from those who fail to survive and reproduce**. Thus, for the process of natural selection to cause evolution, certain prerequisites (=assumptions) must be met.

1. Variation in phenotype

Without **phenotypic variation** in a population there is nothing for the environment to select. In sexually reproducing species, no two individuals are phenotypically identical. Some of this variation can be due to genetic influence, e.g., flower color and vine length in pea plants. Another source of individual variation, however, is some influence of the environment in which the individual develops, e.g., weight differences between individuals due to nutritional differences. Your physical appearance changes throughout your lifetime, but your genetic constitution doesn't change (remember that all of your cells are the product of mitosis and so they are genetically identical). These differences in your appearance are the result of environmental influences. Thus, **PHENOTYPE = GENETIC INFLUENCE + ENVIRONMENTAL INFLUENCE**. These two influences act together in the complex process of development to produce the final adult phenotype. The process of natural selection can act as long as there exists individual phenotypic differences in a population.

2. Variation in genotype

If phenotypic variation exists due to non-genetic (environmental) factors, then selection can occur but will have no evolutionary significance because all individuals will be genetically identical. Differential reproduction of these phenotypic variants will not change gene frequency in the next gene pool. Non-genetic production of phenotypic difference results in an **environmental modification** that must be clearly recognized as distinct from genetically

mediated phenotypic difference because the theory of natural selection requires **genotypic variation** underlying phenotypic variation. We tend to think that genes produce fixed traits as we saw in Mendel's work. This is not true. Each gene will produce a range of phenotypic expressions depending upon the environmental influences to which the organism is exposed during development. For example, if two cuttings are taken from the same tree with one planted in a sheltered lowland, while the other is planted at the tree line on a mountaintop, as adults these two trees will be totally different in appearance. The lowland tree will be large with luxuriant leaves, while the mountain tree will be short and scraggy. Since these two trees are genetically identical, the difference in phenotype (called an environmental modification - see notes on *Environment and Variation* for more detail) must have been due to the environmental influences over gene expression as the trees grew up. **For natural selection to cause evolution, the individuals selected on the basis of their phenotype must be genetically different from those with phenotypes not selected.**

3. Variation in fitness (= reproductive success)

Finally, even if all individuals in a population differ phenotypically and genotypically, the process of natural selection will not cause evolution unless individuals differ in reproductive success (**fitness variation**). Note that the process of natural selection is one of differential reproduction, so if there is no fitness variation, then by definition there can be no natural selection. Given variation in genotype and phenotype, if all individuals leave the same number of offspring, then the composition of the gene pool will not change between generations. Hence, **the theory of natural selection assumes individual variation in phenotype, genotype and fitness**. If any one of the three forms of individual variation is missing, then evolution by the process of natural selection cannot occur.

Would evolution occur if there existed genotypic and fitness variation, but no phenotypic variation? Since different genes can produce identical phenotypes if the phenotypes are under strong selective pressure, the answer to the above question is YES; but the cause of this evolution would be **genetic drift, not natural selection**. The reason some of these genetic variants would leave more offspring than others would have to be due to chance, not to the adaptive significance of their phenotype. Genetic drift, thus, results in **neutrally adaptive (sometimes called non-adaptive (but I hate that term) evolution**.

NATURAL SELECTION AS THE CREATOR OF ADAPTATION

The process of natural selection results in **directed**, rather than random (= **chance**), change in evolution and therefore is considered to be the most significant of the four evolutionary factors. In producing **adaptation** gradually over a number of generations, natural selection is a **creative force** in evolution - a point emphasized by Darwin but not fully appreciated by his critics. **Most**

people appreciate how natural selection can remove the unfit thereby acting as an **erosive force**, but fail to understand how it can produce the fit. For this reason, Darwin's theory did not gain prominence until rather recently. After the rediscovery of Mendel's laws at the turn of the century and the development of genetics as a science, one would have thought that Darwin's theory would have gained immediate acceptance as the major force in evolution. After all, Mendel's work provided the information to vindicate Darwin's assumption of heritability behind adaptive variants (see point 5 in his rationale). Unfortunately, due to the influence of Hugo DeVries, one of the re-discoverers of Mendel's work, the early geneticists emphasized mutation as the mechanism behind the origin of species and relegated natural selection to the minor role of removing unfit individuals (the erosive action of natural selection). Darwin insisted, however, that natural selection created the fit rather than simply removing the unfit and so was responsible for gradual change in a species resulting in the evolution of adaptation.

Natural selection acts as a creative force by preserving in a population individuals who are better adapted to that environment than others (the unfit which are removed). By preserving the better-adapted individuals, selection indirectly preserves those genes that produced the adapted phenotypes, while eliminating genes that produced unfit phenotypes. **Due to the process of sexual reproduction, parental genes are shuffled into new combinations among their offspring to produce a range of individual variation.** Some offspring will therefore be less adapted than their parents, some equal in adaptation to their parents, but, and this is the important point, some will be better adapted. These better-adapted offspring will then be selected as parents in the next generation and the process will be repeated. Gradually, the process of natural selection will improve adaptations so that after many generations **it can be said that the process of natural selection produced the adaptation.**

Creationists often raise the objection that early stages in the origin of an adaptation via natural selection would have no benefit and so they argue that adaptations are created in their fully perfected form. How could a less than perfect eye benefit an individual? Even a moment's objective reflection on this problem (something creationists seem incapable of) will provide several answers. For instance, a less than perfect eye is an improvement over no eyes at all! Moreover, the original elaboration of a structure may have little if anything to do with their present use. For instance, wings could have evolved first as display devices and only later taken on a flight function. Thus, each stage in the evolution of an adaptation confers a reproductive advantage on its possessor over lesser-adapted variants and so gradually over time **natural selection directs evolution by producing adaptation.**

EVIDENCE FOR THE THEORY OF NATURAL SELECTION

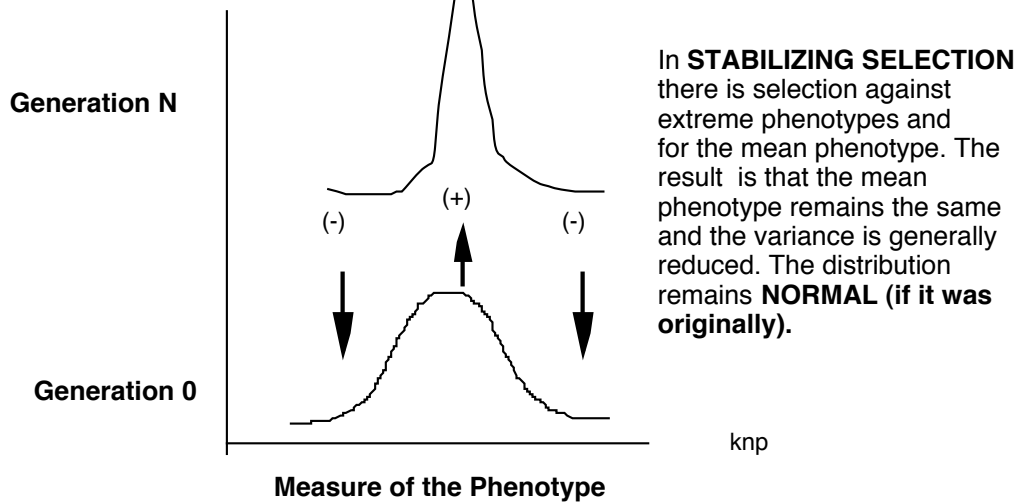
As we have previously discussed, the theory of natural selection requires an ample supply of genetically based phenotypic variation in a population. For asexually reproducing species this variation can only come from mutation, but for sexually reproducing ones independent assortment, recombination and syngamy provide a much greater reservoir of individual variation upon which selection can act. Not all forms of phenotypic variation in a population, however, can be used to demonstrate that the process of natural selection can cause evolution.

Environmental modifications are phenotypic differences between genetically identical individuals due to environmental influences experienced during the process of development and this form of phenotypic variation must be excluded from consideration under natural selection theory as we discussed in the last topic. Examples would be size differences between individuals due to nutritional differences, behavioral differences due to learning, and age-related differences (e.g., tadpole vs. frog). $\text{PHENOTYPE} = \text{GENOTYPE} + \text{ENVIRONMENT}$ is an important concept because it explains how phenotypes arise during the process of development, thus, phenotypic variation in a population can be due to environmental influences as well as genetic influences. Do not assume that because two individuals are phenotypically different that they are also genetically different; the difference in phenotype could be an ENVIRONMENTAL MODIFICATION.

Selection and Continuous vs. Discontinuous Variation

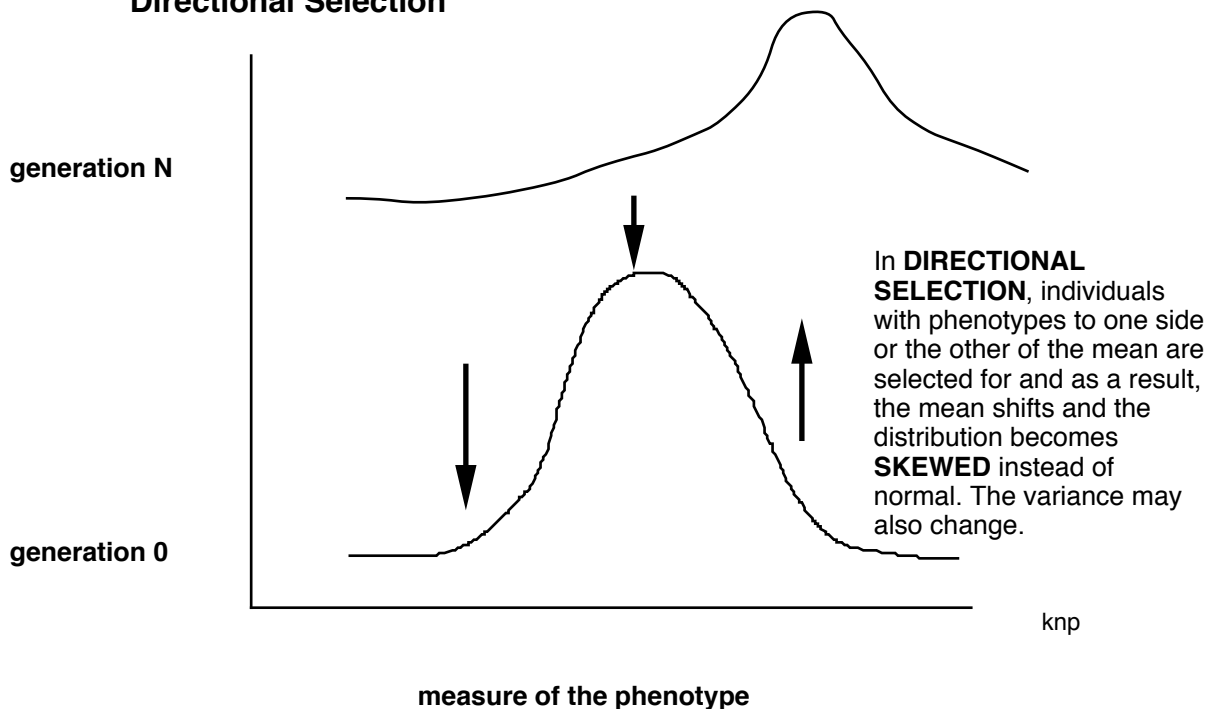
Natural selection can act on both continuous and discontinuous phenotypic variation. **Continuous variation** is under **polygenic** control (many genes contributing to the same trait) and often fits a bell-shaped or normal distribution when the number of individuals is plotted against the range of some phenotypic variable, e.g., height or weight. Three patterns of phenotypic change due to natural selection have been described for a continuously distributed variable. **Normalizing (or stabilizing) selection** favors the average individual in the population and so eliminates the extremes.

Stabilizing Selection

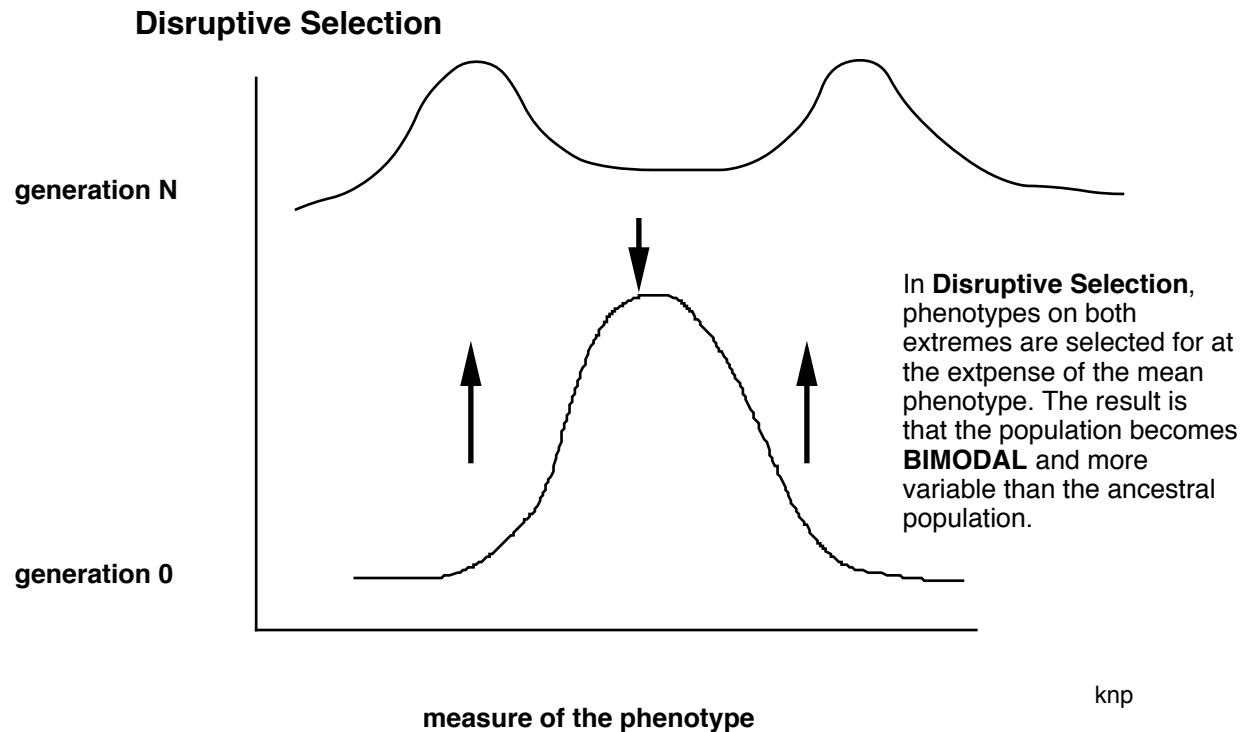


Over time the mean of the population will be preserved but the variance (range of variation on either side of the mean) will be reduced. **Progressive or directional selection** favors one extreme or tail of the distribution and so over time causes a shift in the mean of the population toward the tail that is being selected. This is shown on the top of the next page:

Directional Selection



Finally, **disruptive selection** favors both extremes or tails and so over time the population becomes bimodal and eventually splits into two separate distributions as the average individuals in the population are eliminated.



Let us repeat one caveat. Observation of any of these patterns of phenotypic change in a population does not allow the observer to conclude that evolution has occurred. Why not? The reason is that the phenotypic differences could be due to environmental modification, not genetic difference.

TEST OF THE THEORY OF NATURAL SELECTION

How can one empirically test the theory of natural selection? The answer is **by studying discontinuous variation (= polymorphism)** wherein the difference between the discrete, discontinuous phenotypes can often be reduced to a difference in genotypic combinations of two allelic variants of a single locus; in short, polymorphism conforms to the one gene model of population genetics and can be analyzed in simple Mendelian fashion. For Mendelian genes underlying discontinuous variation the role of the environment in influencing the development of phenotypic differences between individuals can be ignored so that the phenotypic differences between morphs can be considered to be the direct product of the genotypic difference.

Evidence supporting Natural Selection Theory

The one gene model of population genetics predicts the existence of two forms of polymorphism resulting from the action of natural selection:

Transient polymorphism
Balanced polymorphism

According to the one gene model, a population should contain three genetic variants (AA, Aa and aa) that appear phenotypically as two forms or morphs since AA and Aa individuals will share the same phenotype. If selection favors one of the two morphs, the polymorphism will be short-lived or **transient** because selection will eventually eliminate one and so fix the alternative allele in the population. The amount of time needed to eliminate the dominant allele (A) if the recessive phenotype is favored will be much less than that needed to eliminate the recessive allele that is protected in the heterozygous condition (Aa). If, however, selection favors the heterozygote over both homozygotes, then both alleles will be retained in the population in a **balanced** condition.

The process of natural selection can (1) remove or (2) preserve, but not produce genetic variation. In the first case (**transient polymorphism**) natural selection is acting as an **erosive force to eliminate** altogether one of the two alternative alleles. In the second (**balanced polymorphism**) selection is acting as a **creative force to preserve** genetic variation. In preserving genetic variation in a polygenic system, natural selection can increase the probability that sexual reproduction will produce offspring that are more fit than either parent and so create the fit. This last point is crucial to Darwin's concept of natural selection and was discussed at length in the last topic under the heading of *Natural selection as the creator of adaptation.*

Many examples of polymorphism or discontinuous variation can be found in natural populations, but only rarely will the difference between two forms be so crucial to survival and reproductive success that the phenotypic difference can be acted on by natural selection. Most examples of polymorphism are **adaptively neutral (non-adaptive)** and confer no advantage to either form. Variation over time within a population in the frequency of these adaptively neutral morphs is governed **by chance through the action of genetic drift.**

Rare though they may be, examples of adaptive polymorphism do exist and two outstanding examples serve to verify the one-gene model's predictions of transient and balanced polymorphism, thereby **providing evidence for the theory of natural selection.**

TRANSIENT POLYMORPHISM

The phenomenon of industrial melanism occurs in a number of moth species in Europe and the United States. The British ecological geneticist, E. B. Ford, first called attention to this phenomenon as a way of demonstrating the effect of natural selection in nature (as opposed to artificial selection experiments which have long enjoyed success in the lab). Ford noted that a light colored moth species, *Biston betularia*, occasionally undergoes mutation at a single locus to produce a dark or melanic individual. Since the mutant allele is dominant, any gamete containing this mutant will produce a melanic individual upon syngamy.

The first melanic specimen in this species was found in a collection from Manchester, England dated 1848, but by 1895 about 95% of all collected specimens were dark morphs, referred to as the form *carbonaria*. In a series of

observations and mark-recapture experiments during the 1950s, H. B. D. Kettlewell demonstrated that the two forms (light and dark) were differentially preyed upon by birds. He found that the birds selectively caught and ate more individuals of the form that did not match its background as compared to the one that was camouflaged. In industrialized areas of England where the substrate (walls and tree trunks) upon which the moths rested were darkened by pollutants in the smoke poured out by factories, the *carbonaria* form possessed a selective advantage. Rural areas, unaffected by pollutants, afforded the light form an adaptive advantage. The environmental change brought on by the industrial revolution did not produce the *carbonaria* form (which presumably appeared from time to time due to recurrent mutation); it only protected the dark moths from **bird predation (the agent of natural selection)**. The fact that the light form still exists in rare numbers in industrialized areas testifies to the amount of time selection requires to eliminate a recessive allele.

BALANCED POLYMORPHISM

Hemoglobin, a pigmented molecule found in red blood cells, exists in two molecular forms: the normal form (**Hbⁿ**) and the mutant form (**Hb^s**) which in homozygous condition results in the disease sickle-cell anemia. The mutant form differs from the normal form in a single amino acid substitution in one of the two polypeptide chains that, along with the color component, constitute the molecule. This molecular difference means that the gene involved in the synthesis of hemoglobin exists in two forms or alleles.

Individuals suffering from sickle-cell anemia (Hb^sHb^s) usually die early in adulthood because distortions in the shape of their red blood cells caused by the mutant hemoglobin block capillaries, thereby causing the death of tissue distal to the blockage. Consequently, there exists a strong selective pressure against this genotype with the result that the mutant allele will be eliminated in much the same way as the allele causing light coloration in the moths described above. In **malaria** infested regions of Africa, however, the two alleles persist in balanced proportions due to the fact that heterozygotes (HbⁿHb^s) are able to resist the **malaria parasite** (which attacks red blood cells) better than individuals homozygous for the normal hemoglobin form and do not suffer from sickle-cell anemia. By favoring heterozygotes (**heterozygote superiority**) over both homozygotes, selection retains the harmful recessive allele in the population causing **balanced polymorphism**. This heterozygote superiority, however, depends upon the existence of malaria in the population.

In both these examples there exists a demonstrable relationship between phenotype and genotype thereby **allowing the frequency of alleles to be calculated from observation of phenotypic frequencies**. Thus, direct observation of a change in phenotypic frequency between successive generations can be taken as evidence of change in allelic frequency. Since these frequency changes can be attributed to environmental conditions which

act as **agents of natural selection**, these two examples support the theory of natural selection.

Questions:

1. Explain why the process of natural selection is defined as differential reproduction rather than differential mortality.
2. Describe the prerequisites (= assumptions) for the process of natural selection to act as an evolutionary force and explain why each is necessary.
3. Relate the concepts of selection acting as a creative and erosive force to the examples of transient and balanced polymorphism. In each instance identify the environmental force that acts as an agent of selection. Explain how natural selection produces adaptation.
5. Distinguish between each of the following:
 - a. chance and direction
 - b. natural selection as a process and a theory
 - c. differential mortality & reproduction
 - d. natural and sexual selection
 - e. normalizing, progressive & disruptive selection
 - f. transient and balanced polymorphism
 - g. selection as a creative and erosive force
 - h. phenotypic, genotypic and fitness variation
6. Identify each of the following:
 - a. non-adaptive evolution
 - b. industrial melanism
 - c. sickle-cell anemia
 - d. adaptation
 - e. agent of selection
 - f. environmental modification
 - g. heterozygote superiority
 - h. genetic drift