

Evolution: The Darwinian Revolutions

BIOEE 2070 / HIST 2870 / STS 2871

DAY & DATE: Wednesday 11 July 2012

READINGS:

- Kaviar, B. (2003) "A history of the eugenics movement at Cornell"
- Mayr, E. (1982) *The Growth of Biological Thought: Diversity, Evolution, and Inheritance*. Cambridge, MA: Harvard University Press, Chapter 12, pages 535-570
- Ruse/Darwin and Design: *Does Evolution Have a Purpose?* chapters 7 & 8

Lecture 6:00-7:50: The Modern Evolutionary Synthesis

Section 8:00-9:00: The role of mathematics in science and in evolutionary theory

Announcements:

- **Essay #2 is due next Monday 23 July 2012:**

Please submit it as a Word .doc attached to an email, and paste a copy into the body of the email (just in case).

- **Research project proposals are also due next Monday 23 July 2012:**

If you have decided to submit a research paper instead of essays #2 and #3, you must submit an outline and list of proposed references, again as a Word .doc attached to an email, and paste a copy into the body of the email.

- **Some of the readings for this section of the course are available at the course website:**

Behe, M. (1998) Intelligent design as an alternative explanation for the existence of biomolecular machines (unpublished manuscript)

Dobzhansky, T. (1973) Nothing in biology makes sense except in the light of evolution. *American Biology Teacher*, March 1973, volume 35 pages 125 to 129

Kaviar, B. (2003) A history of the eugenics movement at Cornell. 2003 Tallman Prize winner. (unpublished manuscript)

Mayr, E. (1982) *The Growth of Biological Thought: Diversity, Evolution, and Inheritance*, chapters 12 and 13

Provine, W. (1971) *The Origins of Theoretical Population Genetics*, chapter 5

Look for them in the "Course Packets" section of the course website at

<http://evolution.freehostia.com/course-packet/>

The password for the course packets is:

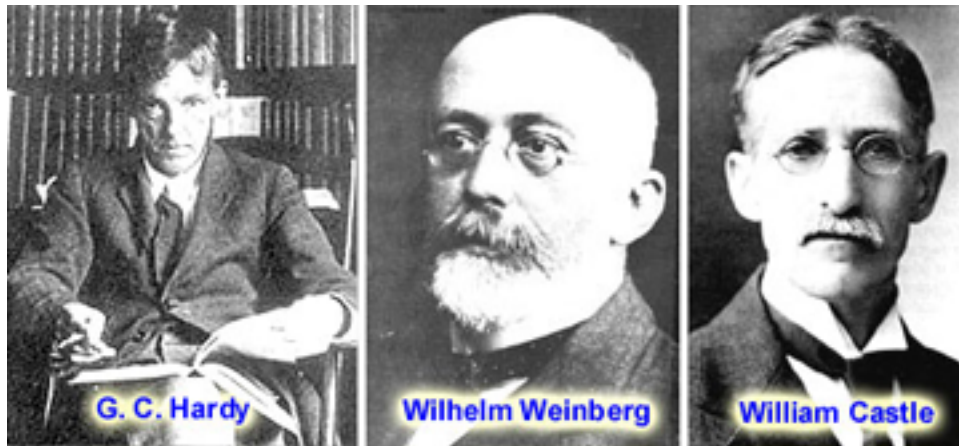
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The Modern Evolutionary Synthesis

The Hardy-Weinberg Equilibrium Law

At the end of the 19th century many commentators declared that "Darwinism" was "dead". However, like Mark Twain, reports of Darwinism's death were "greatly exaggerated." In the second decade of the 20th century, three other researchers, again working separately and mostly unbeknownst to each other, proposed a theory that would eventually lead to the re-establishment of natural selection as the prime mover of evolution.

As described in the reading, [G. H. Hardy](#), [Wilhelm Weinberg](#), and [William Castle](#) all proposed a mathematical theory that describes in detail the conditions that must be met for evolution to **not** occur. This theory, often called **the Hardy-Weinberg Equilibrium Law**, **lays out the conditions that must be met for there to be no changes in the allele frequency in a population of interbreeding organisms over time.**



Recall Mendel's definition of **alleles**: **different forms of a gene that produce different forms of a trait**. In the context of evolution, alleles are what code for the phenotypes that change over time in an evolving population. Therefore, changes in the alleles present in a population will produce changes in the phenotypes present in that population. This, in a nutshell, is:

- **the genetic definition of evolution: changes in allele frequency in a population over time.**

Contrast this with:

- **Darwin's definition of evolution: changes in the characteristics in a population over time.**

What Hardy, Weinberg, and Castle all realized is that for allele frequencies to **not** change in a population, five conditions must be met:

- **There must be no mutations** (*i.e.* alleles cannot change into other, different alleles)
- **There can be no gene flow** (*i.e.* individuals cannot enter or leave the population)
- **The population must be very large** (*i.e.* random changes cannot alter allele frequencies)

- **Survival must be random** (*i.e.* there can be no natural selection)
- **Reproduction must be random** (*i.e.* there can be no sexual selection)

To visualize why these five conditions must be met for evolution to **not** occur, consider a population of 50 flowers in which there are two alleles for one gene controlling flower color:

R = red flowers
r = white flowers

Consider further a population in which 25 of the flowers are homozygous for red flowers (*i.e.* RR) and 25 of the flowers are homozygous for white flowers (*i.e.* rr). This means that the frequency of the two alleles in this population are equal:

R = red flowers = 0.5 = 50%
r = white flowers = 0.5 = 50%

Now, let's see what will happen if the flowers are allowed to randomly interbreed (*i.e.* exchange alleles with each other). We can model this by imagining that all of the alleles are thrown together into a pile, and then they are randomly drawn out two at a time to form the genotypes for 50 new flowers. What would the new distribution of allele frequencies and genotype frequencies be after this happens?

To figure out what will happen, consider the probabilities of drawing different combinations of red and white alleles (you can imagine them as red and white marbles if you wish). There are a total of 100 alleles in the population: 50 red and 50 white. Therefore, for each allele that is drawn, the probability of choosing a red is 50% and the probability of choosing a white is also 50%. These choices are independent of each other, so the probability of choosing pairs of alleles becomes:

RR = 0.5 X 0.5 = 0.25 red flowers
Rr = 0.5 X 0.5 = 0.25 red flowers
rR = 0.5 X 0.5 = 0.25 red flowers
rr = 0.5 X 0.5 = 0.25 white flowers

Notice what has happened: we have gone from a population in which one half of the flowers are red and one half are white, to a population in which three-fourths of the flowers are red and one-fourth are white. It looks like red flowers (*i.e.* the dominant phenotype) is becoming more common, while the white flowers (*i.e.* the recessive phenotype) is becoming less common, and therefore red flowers should eventually completely replace white flowers.

However, notice a crucial point: **none of the alleles has disappeared; they have simply been redistributed.** Therefore, if the five conditions list earlier for a Hardy-Weinberg equilibrium have been met (*i.e.* no mutations or gene flow, large population, and random survival and reproduction), then every time this exercise is repeated from now on, the same genotype frequencies (and therefore the same phenotype frequencies) will be obtained:

$$\begin{aligned}RR &= 0.5 \times 0.5 = 0.25 \text{ red flowers} \\Rr &= 0.5 \times 0.5 = 0.25 \text{ red flowers} \\rR &= 0.5 \times 0.5 = 0.25 \text{ red flowers} \\rr &= 0.5 \times 0.5 = 0.25 \text{ white flowers}\end{aligned}$$

Therefore, **there will be no change in allele frequency in the population over time, and therefore evolution will not have occurred.**

So what? All the [Hardy-Weinberg Equilibrium Law](#) seems to say is that there are conditions under which evolution can't happen? Aren't we interested in those conditions in which evolution can happen? Yes, but notice what the [Hardy-Weinberg Equilibrium Law](#) gives us: it outlines exactly what processes are essential to prevent evolution, and therefore **by negation** shows us how evolution **can** happen.

That is, if any of the five conditions for maintaining a Hardy-Weinberg equilibrium are **not** met, then evolution **must** be occurring. And, of course, virtually none of these conditions is never permanently met in any known natural population of organisms:

- **Mutations occur at a slow but steady rate in all known populations**
- **Many organisms, especially animals, enter (immigration) and leave (emigration) populations**
- **Most populations are not large enough to avoid random changes in allele frequencies**
- **Survival is virtually never random**
- **Reproduction in organisms that can choose their mates is also virtually never random**

Therefore, according to the [Hardy-Weinberg Equilibrium Law](#), evolution must be occurring in virtually every population of living organisms. It is, in other words, as inescapable as gravity.

What is the "engine" of evolution?

The Hardy-Weinberg Equilibrium Law not only shows us that evolution is always and everywhere occurring, it also helps to show which of the factors listed is the most important in causing evolutionary change in which groups of organisms.

For example, although **mutations** are always occurring, they do not occur often enough to cause the kinds of changes that characterize most observed evolutionary change. Mutations, in other words, provide the raw material (i.e. the "fuel") for the engine of evolution, but are not the engine itself.

Gene flow is often restricted in organisms that cannot move around, such as fungi and plants. However, even among them, genetic material gets moved from place to place. And, of course, in animals gene flow is almost always a significant cause of deviations from previous allele frequencies. However, as we will see when we discuss **speciation**, the effects of gene flow and its restriction are not as simple as they might seem at first.

As for **population size**, most actual breeding populations of organisms are not large enough to ensure that there will be no changes in allele frequencies as the result of purely random accidents (*i.e.* "sampling error"). Indeed, a previously undiscovered form of evolution, called **genetic drift**, was proposed to occur whenever populations are small enough for random accidents to cause changes in allele frequencies. This process, sometimes called the "Sewall Wright effect" for its discoverer, will be discussed later in this course.

As you might suspect, **survival is virtually never random**. It should be clear by now that non-random survival is just another name for natural selection, Darwin's original engine of evolutionary change. As a result of the formulation and widespread acceptance of the Hardy-Weinberg Equilibrium Law and its mathematical implications, **natural selection** was once again proclaimed the primary engine of evolution.

However, there is another engine, at least among animals. Like survival, reproduction (*i.e.* courtship, mating, birth, development, etc.) is virtually never random among animals, especially land animals who can choose who they mate with. Therefore, **sexual selection** is also an important engine of evolution in animals (and even in some plants).

The **Hardy-Weinberg Equilibrium Law** provided more than just a "null hypothesis" for genetic evolution. As we will see, it provided a mathematical basis for a more comprehensive theory of evolution in which natural selection, Mendelian genetics, paleontology, and comparative anatomy were combined in what is now known as the "**modern evolutionary synthesis**."

R. A. Fisher and the Fundamental Theorem of Natural Selection



(Sir) [Ronald Aylmer Fisher](#) built on the pioneering theoretical work of [Hardy](#), [Weinberg](#), and [Castle](#) by providing mathematical models that further undermined the [Mendelian geneticists'](#) theory of [evolution via macromutation](#). He did this by showing that continuous variation could provide the basis for natural selection as proposed by Darwin. In his most important work, [The Genetical Theory of Natural Selection](#) (published in 1930) Fisher showed that traits characterized by continuous variation (*i.e.* those that approximate a normal, or bell-shaped, distribution) were both common and could provide all the raw material necessary for Darwinian natural selection. This is because such traits, although being continuous in populations, do *not* blend from parents to offspring. Instead, as Mendel first showed, they are produced by unblending "particles" of inheritance (*i.e.* Mendelian "genes"). In other words,

- **Mendelian inheritance conserves, rather than eventually destroying, the genetic variation that exists in natural populations.**

Fisher then proposed his [fundamental theorem of natural selection](#), which states that:

- **The rate of increase in fitness of any organism at any time is equal to its genetic variance in fitness at that time.**

Essentially, Fisher's theorem says that the degree of change that can result from natural selection depends fundamentally on the amount of genetic variation present in the population undergoing selection. If there is very little variation, then natural selection cannot change the characteristics of the members of the population very much. Conversely, if there is a lot of genetic variation, this can form the basis for considerable evolutionary change as the result of natural selection.

Fisher proposed that most of the variation required for natural selection to occur is "hidden" in heterozygotes in populations. His logic went something like this:

- Selection against dominant alleles (which is equivalent to selection for recessive alleles) should remove dominant alleles from populations almost immediately

- Selection against recessive alleles (including almost all mutations, which are usually deleterious) should reduce their frequency until they are “hidden” among heterozygotes
- If selection shifts, so that a recessive allele now becomes favorable, it can increase in frequency quickly (since dominant alleles would now disappear rapidly)
- Therefore, the more hidden recessive alleles there are in a population, the more rapidly selection can “bring them forward” if the environment shifts and makes them beneficial
- By implication, the larger a population is, the more recessive alleles can be hidden in it
- Therefore, natural selection works faster and more effectively in large populations in which there is lots of heterozygosity hiding recessive alleles

Fisher’s theorem, although modified somewhat today, forms the basis for much of modern evolutionary theory. It also parallels an observation made by Darwin in the [*Origin of Species*](#): **the more widespread and variable a species is, the greater the effects of natural selection will be in that species.** Fisher's theorem is a mathematical explanation of Darwin's observation about the variability of organisms in natural populations.

Sewall Wright, Random Genetic Drift, and Adaptive Landscapes

R. A. Fisher's fundamental theorem of natural selection formed the basis for a mathematical theory of evolution in which the process of natural selection is modeled mathematically in the same way that Newton modeled the force of gravity. Indeed, Fisher pointed out several times that the mathematics of natural selection were similar in many ways to such physical models as the ideal gas laws and the second law of thermodynamics. According to his mathematical models, alleles that were positively selected would increase in frequency in populations in much the same way as gas molecules spread out in an expanding balloon.

To many evolutionary biologists, this meant that natural selection would inevitably result in "fixation" of alleles that were not selected against. That is,

Any allele that results in increased survival and reproduction should, if given enough time, eventually become the only allele for that particular trait.

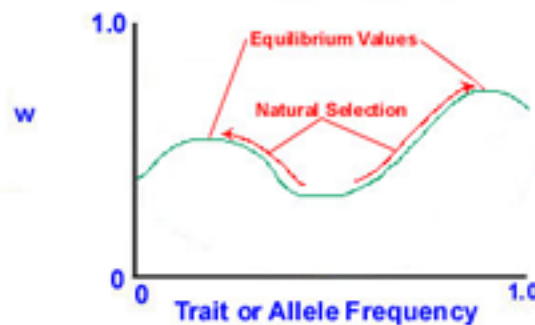
This presented a problem to evolutionary biologists that was almost as severe as the "mutationism" of the early Mendelians. It implied that the inevitable result of natural selection would be the eventual elimination of all non-adaptive variation in natural populations. This would then cause natural selection to grind to a halt (or to become reduced to essentially the rate of production of new genetic mutations, which is slow in the extreme, much slower than the observed rate of evolution).

A solution to this problem was provided by Sewall Wright, who discovered a process that has become known as random genetic drift (or simply genetic drift). Wright, who worked primarily with domesticated animals in controlled breeding programs, proposed that in small populations of organisms, random sampling errors could cause significant changes in allele frequencies in those populations. He showed mathematically that the smaller a population was, the greater the effect of such random events on its allele frequencies. In other words, evolution could proceed by at least two primary mechanisms: Darwinian natural selection and random genetic drift.



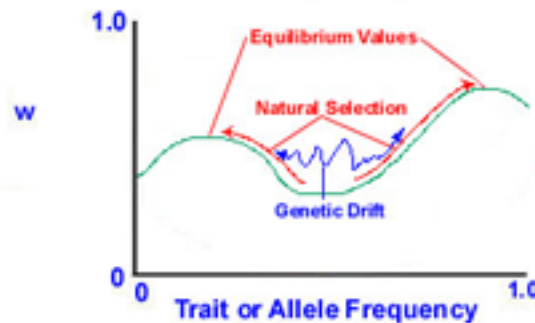
Sewall Wright (and friend)

Wright then went on to develop a formal model for [genetic evolution](#) in which the [allele frequencies](#) present in a [population](#) were visualized as forming an [adaptive landscape](#). In Wright's model, the [allele frequencies](#) present in a [population](#) were visualized as elevations in a topographical surface, similar to the lines of elevation in a [topographic map](#). According to the prevailing theory at the time, selection could only cause [allele frequencies](#) to ascend adaptive "peaks" in such a landscape, never descend into the "valleys" of [maladaptation](#). This meant that selection alone could only result in [fixation](#) and eventual genetic stagnation.



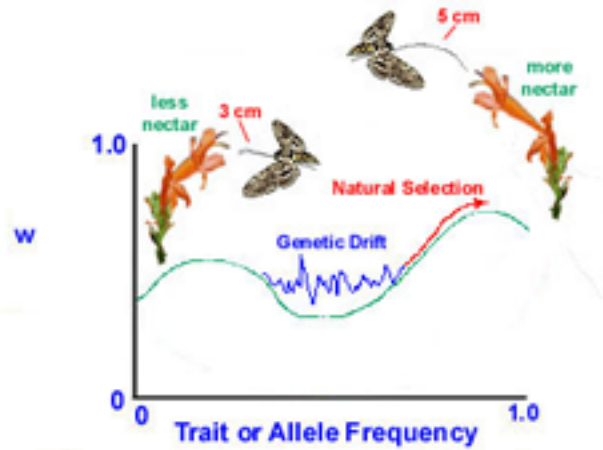
Results of Selection Alone

What Wright showed is that [genetic drift](#) could, in small populations, cause [allele frequencies](#) to drift from one adaptive peak to another, and in this way could keep evolution by [natural selection](#) moving. He called this theory the "[shifting balance theory of evolution](#)", as it emphasized the shift from one adaptive peak to another by means of [random genetic drift](#).



Results of Selection and Genetic Drift

We can visualize how this process works by considering a population of moths that are adapted to foraging for nectar in trumpet flowers. These moths need long tongues to reach the nectar in the base of the flowers. Consider a population of moths with tongues that average 3 cm in length. These moths can reach the nectar in short-necked trumpet flowers, but cannot reach the nectar in longer flowers. It would be better for the moths to have longer tongues. However, selection in this case would tend to cause the mean value for tongue length in the moths to peak at about 3 cm. There is another "theoretical" peak at 5 cm, but selection by itself would not allow for an increase in tongue length.



Results of Selection and Genetic Drift

However, if the population of moths with 3 cm tongues can "drift" across the "valley" between the adaptive peaks at 3 cm and 5 cm, selection can begin to shift the moths with longer tongues toward the higher adaptive peak. In this way, selection and drift working together can result in a shift in adaptiveness that could not have occurred by selection alone.

J. B. S. Haldane and *The Causes of Evolution*



John Burdon Sanderson Haldane (usually referred to as [J. B. S. Haldane](#)) finalized the revolution in theoretical population genetics begun by Hardy, Weinberg, Castle, Fisher, and Wright. In his most important book, [The Causes of Evolution](#), published in 1932, he showed that genetic mutations such as those observed by de Vries and the early Mendelians, could provide the raw material for Darwinian natural selection. Furthermore, he showed mathematically that such mutations could do this even when their frequency in a population was initially so low that they would be "invisible" to statistical analysis. He also showed how dominance could evolve in populations by means of natural selection, even when the original expression of an allele was initially recessive.

Although Haldane did not propose any single theory that could be called revolutionary, his approach, like that of his predecessors, was. In particular, Haldane stated

"The permeation of biology by mathematics is only beginning, but unless the history of science is an inadequate guide, it will continue, and the investigations here summarized represent the beginning of a new branch of applied mathematics."

- J. B. S. Haldane (1932) [The Causes of Evolution](#), page 215

Haldane is also remembered for two quips that are often repeated by evolutionary biologists. The first concerns a question posed to him by an Anglican minister, who asked him (supposedly at a dinner party) what his study of nature had led him to conclude about the principle concern of the Creator. Without batting an eyelash, Haldane replied:

"An inordinate fondness for beetles."

referring to the fact that there are more species of beetles on Earth than any other kind of organism).

During another conversation (supposedly in a pub), Haldane was confronted with the observation that natural selection should result in pure selfishness on the part of individuals, and therefore no one should be willing to risk his own life to save another. To this Haldane replied,

"I would be willing to risk my life to save two brothers or eight cousins."

This quip is based upon the observation that brothers share an average of one-half of their genetic material, whereas first cousins share an average of one-eighth. Therefore, saving two brothers or four cousins would result in the same genetic contribution to the next generation as that represented by one's own genome. This quip was later cited by one of the founders of what is now known as the theory of [kin selection](#), in which natural selection is considered to act at the level of genes, rather than individuals. We will discuss this idea in a later lecture.

Theodosius Dobzhansky and *Genetics and the Origin of Species*

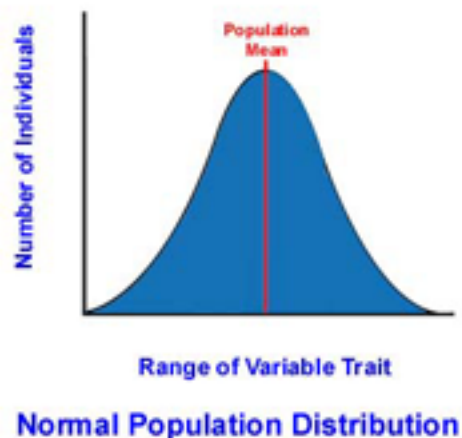
R. A. Fisher, J. B. S. Haldane, and Sewall Wright are usually recognized as having laid the theoretical foundation for modern evolutionary theory. However, many evolutionary biologists and historians of science consider that the "modern evolutionary synthesis" was initiated by Theodosius Dobzhansky with the publication of his most famous book, *Genetics and the Origin of Species*, published in 1937.



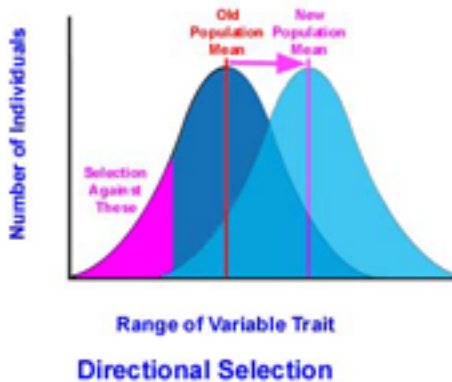
Dobzhansky combined the Mendelian genetics, the mathematical models of Fisher, Haldane, and Wright, and the observations of natural selection in the wild in a theory that reinstated natural selection as the primary engine of evolution. He emphasized both the scientific aspects of evolutionary theory, and the implications of evolutionary theory for education and society in general.

Among Dobzhansky's important contributions to the modern theory of evolution by natural selection is his analysis of the three different patterns of evolutionary change that can result from natural selection. According to Dobzhansky, there are three general types of natural selection: directional selection, stabilizing selection, and disruptive selection.

To visualize each type, begin by considering the pattern of variation in a typical trait, such as beak length in finches. In such a population, there is a natural (*i.e.* random) variation in this trait, which is arrayed along the X axis. The number of individuals showing a particular value of this trait is arrayed along the Y axis. The result approximates a bell-shaped curve (*i.e.* a "normal distribution") in which finches with intermediate sized beaks are the most common in the population, while finches with very large or very small beaks are much less common:



Consider the effect on the mean value of this trait in the population if individuals at one or the other (but not both) extreme of expression of this trait are selected against (i.e. have lowered survival and/or reproductive success). The result will be a shift in the mean value for the trait in the population:



Such a shift in the mean value for a particular trait in any population is a tip-off that selection is occurring in that population. Since the overall effect of such selection is to cause a uni-directional shift in the mean population value, this kind of selection is called directional selection.

- An example of directional selection is the increase in mean beak size among Galapagos finches as the result of prolonged drought.

Now consider a similar population in which selection is exerted most strongly against individuals at both extremes of the range of variation in a particular trait. The result of such selection would be no change in the overall population mean, and a tightening of the range of variation in the population:

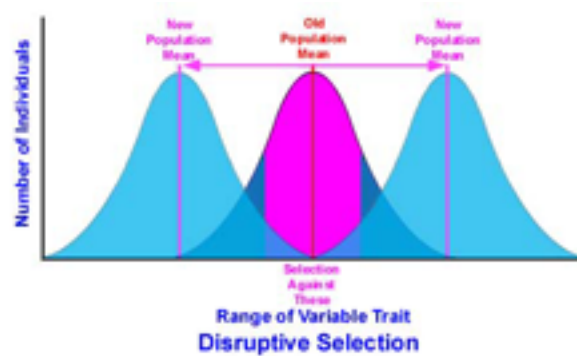


Since the overall effect of such selection is to maintain the trait in question at or around the previously existing population mean, this kind of selection is called stabilizing selection.

- Stabilizing selection can have important implications for later evolutionary change, as the decrease in overall variance in the trait in question can limit the amount of change that can occur later if selection is relaxed. In essence, **once a population has been subjected to intense stabilizing selection, it is much less likely to shift later as the result of a change in the environment.**

- An example of stabilizing selection in humans is shown by the relationship between birth weight and mortality. There is increased mortality at both extremes of birth weight, which causes a tightening of the normal distribution of birth weights. Such a narrowing of mean birth weight is more intense in poor environments, and less intense in richer ones.

Finally, consider a population in which selection is exerted most strongly against individuals in the middle of the range of variation, which is usually the largest fraction of the population. The effects of such selection would be the production of a bimodal distribution of the trait under selection:



The result of such selection is a dramatic increase in the amount of variance in the trait in the population, and the "splitting" of the population into two distinct sub-populations, each with its own characteristic mean value for the character in question. Because the mean population value is eliminated and replaced by two different means, this kind of selection is called [disruptive selection](#).

- [Disruptive selection](#) is sometimes called *diversifying selection*, as it results in the production of increased diversity of traits in populations. As such, diversifying selection has been implicated in evolutionary divergence, and may be a primary cause of speciation (we will discuss this in a later lecture).
- An example of disruptive/diversifying selection is the distribution of beak sizes in [African seedcrackers](#). There is a clearly bimodal distribution of beak sizes among these birds, corresponding to two different sub-populations of seedcrackers that specialize in eating either small or large seeds.



In a famous essay entitled "[nothing in biology makes sense except in the light of evolution](#)," Dobzhansky showed how [modern synthetic evolutionary theory](#) provides a comprehensive explanation for the origin and evolution of life on Earth.

George Gaylord Simpson and *Tempo and Mode in Evolution*

So far, all of the contributors to the “modern evolutionary synthesis” have been geneticists or population geneticists. However, scientists from other disciplines also contributed to the synthetic theory. Principle among these was [George Gaylord Simpson](#), curator of the departments of geology and paleontology at the [American Museum of Natural History](#) in New York, and later curator of the [Museum of Comparative Zoology](#) at Harvard University in Cambridge, Massachusetts.



Simpson was a [paleontologist](#); that is, a scientist who studies ancient (and often extinct) organisms, usually by studying their fossils and other remains. He was an expert in comparative anatomy, particularly of mammals, and most especially of horses and their evolutionary ancestors. In his most important book, *[Tempo and Mode in Evolution](#)* (published in 1944), Simpson presented two major concepts that were essential to the modern evolutionary synthesis:

- The idea that the fossil record generally supports the theories presented by population geneticists, especially Fisher, Haldane, Wright, and Dobzhansky, and
- The observation, based primarily on the fossil record, that the pace at which evolution has occurred has varied over geologic time.

The first idea – that the fossil record generally supports the theories of population genetics, was probably less important in the long run than the second. The reason for this was that Simpson’s suggestion that the rate of evolutionary change could speed up or slow down seemed to some evolutionary biologists to depart somewhat from Darwin’s theory, which most evolutionary biologists interpreted as saying that evolution was both continuous and gradual. As we will see, this idea was challenged in 1972 by [Niles Eldredge](#) and [Stephen J. Gould](#) in their landmark paper on [punctuated equilibrium](#) (downloadable from the [course packet at the course website](#)). This development was particularly ironic, as Simpson is usually credited with bringing paleontology into the “modern evolutionary synthesis”, whereas Eldredge and Gould are perhaps the most famous challengers to that same synthesis.