Natural Selection

For natural selection to produce a change in the composition of a population there must be
• phenotypic variation
• heritability of variation
• differential reproductive success of different phenotypes

Differential survival and reproduction has been demonstrated in the wild and in the laboratory many times.
Ex 1. *Brassica rapa* - resistance to drought - more sporadic and smaller amounts of rainfall results in shorter time periods for plants to flower and reproduce.

Drought conditions began in S. California in 2000 and persisted through 2004. Seeds collected in 1997 were used to produce a new generation and then a second generation under favorable conditions.

Seeds collected in 2004 grown under the same conditions exhibited a shorter life cycle.
Variation in flowering time is apparent

Heritability is established through hybridization and rearing under the same conditions (a common garden study)

The potential for differences in reproductive success is clear

Why couldn’t they just establish that the 2004 plants flowered earlier in the field than the plants did in 1997?
Many species have shown that the phenotype seen is the product of the genotype and the environment.

A short time to first flowering may be a physiological response to drought and not due to change in the composition of the population.

*Achillea millefolium*  
Clausen, Keck & Hiesey 1940s
A single genotype can express different phenotypes in different environments. The pattern is called a “norm of reaction.”

*Persicaria maculosa:*

Different genotypes may have different norms of reaction. Some environmentally specific phenotypic changes can promote survival and reproduction.
Read: Natural Selection and Coat Color in the Oldfield Mouse.
**Adaptation** - a feature of an organism that contributes to its reproductive success in a specific environment. It is the product of past natural selection. An increase in reproductive success may be the result of an increase in survival ability, reproductive ability or both.

An adaptation increases the “fit” between an organism and its environment.

It increases “fitness” - its ability to contribute to future generations.
**Exaptation** - a feature of an organism that contributes to its reproductive success in a particular environment but evolved through differential reproductive success under different conditions in the past. It was an adaptation for one environment but now serves a different purpose and contributes to reproductive success.

The classic example of an exaptation is feathers. Today feathers serve at least two purposes in birds - insulation and flight.

The fossil record and estimates of the phylogenetic (evolutionary) relationships of feathered organisms suggests that feathers evolved before flight.
Feathers evolved before flight perhaps as an adaptation associated with thermoregulation.

Later, feathers allowed some organisms to begin gliding and then flying. In this sense, feathers are an exaptation.

Further changes in feather structure were the product of their benefits in flight. The new features of feathers are an adaptation.

Exaptations are sometimes called “preadaptations.”
Read: Natural Selection in the Field

Low-predation site
Females produce fewer but larger offspring

High-predation site
Females produce many small offspring

Predator (Rivulus hartii)
Prey (guppies)

Predator (Crenicichla alta)
Lenski’s long-term evolution experiment: a study of adaptation of *E. coli* over 50,000 generations to constant environmental conditions.

Can measure change in fitness by comparing the competitive ability of cells relative to their original ancestors.
Over time, cell lines became better competitors and increased in size in the laboratory environment.
Over time, the optimal temperature for growth shifted from 40°C to 37°C (the temperature at which they were grown).

Why?

The 37°C adapted line also showed decreased growth relative to their ancestors at higher temperatures (42°C) and lower temperatures (20°C).
Pleiotropic gene - a gene that has multiple effects on the genotype. The gene or genes that control testosterone production in mammals have multiple phenotypic effects.

Antagonistic pleiotropy - a gene may have positive effects on fitness through one or more phenotypic effects while also having negative effects on fitness through other phenotypic effects.

An evolutionary trade-off is a reduction in fitness through one characteristic while gaining fitness through another characteristic.
Physical processes and laws limit what can be produced by natural selection. Each is adapted to different environmental conditions but limited by physical constraints and their evolutionary history.
Allometric relationships are often the result of physical constraints.

Allometric relationships that are curves on an arithmetic scale appear as linear on a logarithmic scale.
The mass or total volume of an organism scales with the cube of any linear measure of size.

The strength of structures scales with the square of any linear measure of size.

So, we should expect skeletal features related to support should increase in size faster than overall measures of body size.
Genetic variation decreases under selection.

Flies with no overall preference for flying toward or away from the light can be selected for positive phototaxis or negative phototaxis.

\[ H^2 = 0.09 \]

After many generations of selection the response to selection decreases.

Pure-bred lines have little genetic variation for responding to selection.

Variation within pure-bred lines is mostly or entirely environmental - heritability is very low.
Evolution by natural selection has no foresight.

There is no goal. It produces adaptations for the present situation but cannot anticipate future environmental change.

Natural selection works with variation in genes and phenotypes available now and can only change their frequencies. It can’t go back to the drawing board and develop a better design.
Read: Evolutionary Arms Races

Origin of Complex Traits

“If it could be demonstrated that any complex organ existed, which could not possibly have been formed by numerous, successive, slight modifications, my theory would absolutely break down.” C. Darwin, The Origin of Species, Chap VI
Organs of extreme perfection and complication.—To suppose that the eye, with all its inimitable contrivances for adjusting the focus to different distances, for admitting different amounts of light, and for the correction of spherical and chromatic aberration, could have been formed by natural selection, seems, I freely confess, absurd in the highest possible degree. Yet reason tells me, that if numerous gradations from a perfect and complex eye to one very imperfect and simple, each grade being useful to its possessor, can be shown to exist; if further, the eye does vary ever so slightly, and the variations be inherited, which is certainly the case; and if any variation or modification in the organ be ever useful to an animal under changing conditions of life, then the difficulty of believing that a perfect and complex eye could be formed by natural selection, though insuperable by our imagination, can hardly be considered real. C. Darwin, The Origin of Species, Chap VI
Hypothetical stages in the evolution of a camera eye match observable states in nature.
Novel features and exaptations

Cranial sutures allow brain growth in vertebrates early in development. They later fuse to form the protective cranium.

Cranial sutures allowed the evolution of viviparity in placental mammals.

They are an exaptation or preadaptation for live birth.
Novelty at the Molecular Level

A common challenge to the idea of evolution is the question of how new features and functions originate.

**Gene sharing** - Proteins can have different enzymatic activities under different conditions - e.g. Lens crystallins form the lens of the eye in vertebrates but also serve multiple enzymatic functions in different tissues in different groups.

<table>
<thead>
<tr>
<th>Crystallin</th>
<th>Species</th>
<th>Enzyme</th>
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<tbody>
<tr>
<td>δ</td>
<td>Birds and reptiles</td>
<td>Argininosuccinate lyase</td>
</tr>
<tr>
<td>ε</td>
<td>Birds and crocodiles</td>
<td>Lactate dehydrogenase D4</td>
</tr>
<tr>
<td>τ</td>
<td>Lamprey, fish, reptiles, and birds</td>
<td>α-Enolase</td>
</tr>
<tr>
<td>λ</td>
<td>Rabbit</td>
<td>Hydroxyacyl-CoA dehydrogenase</td>
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<td>ζ</td>
<td>Guinea pig</td>
<td>Alcohol dehydrogenase</td>
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Multiple copies of a single gene can arise through gene duplication. One way gene duplication can occur is through unequal crossing over. Improper synapsis followed by crossing over results in multiple copies of the same gene. Each copy is then free to vary independently and potentially lead to new functions in different tissues or circumstances.
Multiple copies of a gene that ultimately serve different functions are “gene families.”

One of the best known gene families is the globin gene family.

The human β-globin locus is composed of five genes located on a short region of chromosome 11, responsible for the creation of the beta parts the oxygen transport protein Hemoglobin. This locus contains not only the beta globin gene but also delta, gamma-A, gamma-G, and epsilon globin. Expression of all of these genes is controlled by single locus control region and the genes are differentially expressed throughout development.

The human alpha globin gene cluster located on chromosome 16 spans about 30 kb and includes seven alpha like globin genes and pseudogenes: 5'- HBZ - HBZP1 - HBM - HBAP1 - HBA2 - HBA1 - HBQ1 - 3'. The HBA2 (α2) and HBA1 (α1) coding sequences are identical.
Read: Gene duplication and the evolution of the aldosterone receptor.

1. Ancestral receptor binds cortisol (and would have been able to bind aldosterone had it existed)
2. Gene duplication event creates two versions of receptor. Both bind cortisol (and could have bound aldosterone)
3. One receptor loses ability to bind still-nonexistent aldosterone hormone
4. Aldosterone synthesis evolves; suitable receptor is already in place