

Selection: an overview

Natural selection is the centerpiece of Darwin's evolutionary theory. Selection theory explains the manifold adaptations of organisms, the innumerable features and behaviours that equip them to make efficient use of energy resources, defend themselves, survive and reproduce. In this lecture we will establish several important points about selection by considering examples of how selection can impact organismal variation. In the next lecture we then move on to a population genetic theory of natural selection.

What is Natural Selection?

Natural selection is the naturally occurring variation in average reproductive success among phenotypes, including differences in viability (survival to reproductive age), mating success, and fertility. The term "natural" distinguishes it from "artificial" selection by humans. There are several important points to understand about natural selection (recall the basic ingredients of Darwin's theory of Natural Selection).

1. More individuals are produced than can make it to the next generation (**overproduction**). In growing populations where every offspring is recruited to the next generation there will be no selection.
2. **Variation in the phenotype** is a prerequisite and it must be correlated to **reproductive success**.
3. Since "phenotype = genotype + environment", phenotypic variation can be heritable ("genetic") or not heritable ("environmental"). Selection happens irrespective of the nature of variation, but evolution by natural selection can only occur if variation is heritable.
4. **Natural selection \neq evolution**. Evolution is the heritable change of phenotype over time. Natural selection on heritable variation is a factor that drives evolution, but there can be other factors (such as epigenetic trans-generational inheritance) or genetic drift that lead to evolution. Also, natural selection on heritable variation does not necessarily imply evolution (e.g. selection toward a stable optimum).

Fitness (\approx reproductive success)

Fitness is the currency of selection measuring reproductive success. The **absolute fitness** of a phenotype is the average number of surviving offspring in the next generation of individuals with a given phenotype (counted after a full life cycle: zygote to zygote, or adult at reproductive age to adult at reproductive age). **Relative fitness** is a standardized measure expressing reproductive success of a phenotype relative to the phenotype with maximum reproductive output in the population. Importantly, fitness does not only refer to survival as Darwin's famous 'survival of the fittest' may imply. It is a measure of reproductive success including all of its components such as survival or the ability to attract /control/fertilize a mate.

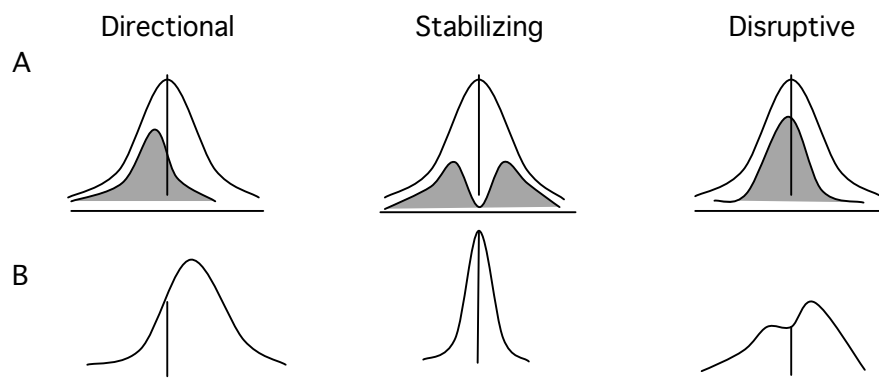
Selection \approx differential fitness

Since one is mostly interested in selection on heritable variation, not just on any phenotypic value, one can also define fitness for genotypes as the average phenotypic fitness of individuals with the same genotype. Similarly, one can define fitness of smaller units, such as alleles, as the average phenotypic fitness of all individuals that carry this allele. It is, however, important to keep in mind that selection is due to fitness differences of heritable phenotypes.

Types of selection

Selecting can act in various ways on phenotypic variation. We tend to assume a Gaussian distribution describing one aspect of a phenotypic character (e.g. height) and describe the type of selection which part of the distribution is preferentially recruited into the next generation.

- 1) **Directional selection:** Selection causing a consistent directional change in the form of a population through time, for example selection for larger body size.
- 2) **Stabilizing selection:** Selection tending to keep the form of a population constant. Individuals with an intermediate value for a character have high fitness; those with extreme values have low fitness, e.g. human birth weight until very recently.
- 3) **Disruptive selection:** Selection favoring forms that deviate in either direction from the population average. For instance, selection favors forms that are larger or smaller than average, but works against the average forms between.



A: phenotype distribution before selection, B: after selection. In shadow, individuals with reduced reproductive success, e.g. that did not survive to reproductive age.

Levels of Selection

Evolution by **natural selection operates on any replicator that produces heritable variation in fitness**. Individual organisms clearly are such replicators, but we can also look on biological life on different levels of organization: Genes, gametes, individuals, families, populations, species, etc. All these are, in an abstract sense, entities that are able to reproduce with changes and hence to evolve under natural selection. Since these levels are coupled in a hierarchy, selective processes at the different levels are not independent, but will interfere and sometimes compete, and eventually collectively produce evolutionary change. It is frequently been asked in evolutionary biology which level (or unit) of selection is important for adaptive evolution. Which level drives evolution and who benefits from it? It turns out that conceptualizing at which level selection acts is a complex issue.

This is well illustrated by cancer where a mutation can introduce a selfish allele (a replicator). In terms of copy numbers, its fitness is increased over that of the wildtype allele. Also, all cells (and associated elements e.g. mitochondrial haplotypes) carrying the mutated allele will increase in fitness. However, due to detrimental effects of uncontrolled growth in a

multicellular organism, the survival of the individual will be compromised and reduce its fitness depending on its reproductive value (i.e. expected future reproduction). We therefore expect selection against mutations causing cancer at an early age, but not at an advanced age where reproductive success can no longer be increased. This example illustrates the often complex interactions of different levels of selection and their dependency on intrinsic (e.g. age) and extrinsic (e.g. environmental) factors.

Here, we will just mention some examples illustrating different properties of selection. Specifically, we consider 4 cases: Apart from the 'default level' of selection on the individual we will consider selection at the level of gametes, populations, and families.

1) Individual selection. We will start with individual selection, the default we generally have in mind when thinking about selection. Individual selection refers to selection on phenotypes (or associated genotypes) that affect the fitness of the individual. Generally, we think of **natural selection** as initially introduced by Darwin where individual variation in fitness is correlated with external biotic or abiotic features. However, Darwin himself soon recognized that natural selection alone can not explain sexually dimorphic features such as exaggerated sexual ornaments (e.g. peacock tail, antlers of deer) that obviously impair survival. In *The Descent of Man, and Selection in Relation to Sex* (Darwin 1871) he introduced the idea of **sexual selection** capitalizing on the idea that reproductive success is not merely determined by survival, but likewise by an individual's ability to attract mates and actually reproduce. Sexual selection often results in **sexual conflict** given a different optimum for male and female for a certain character. E.g. male ducks may be able to increase reproductive success by displaying colourful ornaments, whereas females incubating the eggs would benefit from drab cryptic colouration. This is a very interesting conflict that is played out on the same genome that over generations moves between sexes (except for mitochondria and sex chromosomes). Where this conflict is resolved, **sexual dimorphism** is observed that needs to be encoded on a very similar genome (often only differing by a few genes on sex chromosomes or not at all if sex determination). An extreme example where sexual selection runs counter to natural selection by means of survival is suicide of male redback spiders. The much smaller male redback spider somersaults into the female mouth after copulation and are devoured. Males displaying this behavior are shown to have higher success in siring offspring. This example nicely illustrates that prolonged survival is not necessarily advantageous. Lifetime reproductive success, not survival, is the currency of selection.

Evidence for evolution by (individual) selection. As pointed out above, selection does not necessarily lead to evolution. Evolution will only result if 1) variation in fitness is correlated with variation in the trait of question, 2) selection is directional or disruptive and 3) other forces such as genetic drift do not override the effects of selection. Despite of these constraints there is innumerable evidence that selection plays a large role in phenotypic evolution. **Artificial selection** applied during domestication strikingly demonstrates the power of selection: within less than 200 years, almost the entire phenotypic variation among dog breeds most likely tracing back to a single origin has evolved by strong artificial selection on traits deemed of interest to the human agent. The impact of artificial selection can also be observed in natural populations. Human harvest has induced directional evolutionary change the distribution of maturity age or body size (e.g. Atlantic cod) or horn size (e.g. bighorn sheep). **Experimental evolution** demonstrates that mutations can increase or decrease in frequency over time depending on their fitness under imposed environmental conditions. In

addition, there are numerous examples of evolution by selection in **natural populations** both for natural selection (e.g. selection on coat colour in rock pocket mice¹) and sexual selection (e.g. manipulation experiment in long-tailed widowbird).

2) Gametic selection occurs below the level of the individual. Most adaptations that increase the average number of offspring of an organism will also benefit the gametes, and vice versa. However, at a heterozygote locus (AB) one of the alleles (e.g. A) can adopt a strategy to increase its frequency at expense of the other allele (B) in a way that is independent of the overall number of offspring: With normal Mendelian segregation, half of the organism's offspring will inherit A. In some cases, however, Mendel's law is broken and alleles manage to get into more than 50% of the offspring, a phenomenon called **segregation distortion**. Specifically we refer to **meiotic drive** (genes drive meiosis into a biased outcome) if transmission of the **selfish genetic element** is controlled by female meiosis or **genic drive** if associated with male gametes e.g. through sperm competition).

A standard example is the segregation distorter (sd) gene in *Drosophila melanogaster*. In male flies that are heterozygote for sd, sd manages to get into 90% of all functional sperm (the other sperm is produced but becomes degenerate by the sd mechanism). Obviously, this means a large selective advantage for sd over competing alleles and, everything else being equal, the allele should spread to fixation. It turns out, however, there is a severe fitness cost of sd on the level of the organism: homozygote sd males are infertile and heterozygotes suffer reduced fertility. Therefore, evolution of sd is clearly not in the interest of the organism and all other genes that are not tightly linked to sd. As a consequence, any allele that suppresses segregation distortion by sd will get selected. This leads to the following general pattern for meiotic drive:

Drive alleles that can enter more than 50% of the offspring in heterozygotes have an inherent selective advantage and will initially increase in frequency. Once this occurs, the next step depends on the effect on organismal fitness: If there is no effect on organismal fitness (or even an increase), the allele will sweep to fixation. Since segregation distortion does not operate in homozygotes, the effect will then disappear. If the distortion allele reduces organismal fitness, suppressor alleles at almost any other locus of the genome will be favored and will usually evolve. In either case, selection distortion is short-lived. Rareness of meiotic drive also suggests that it is difficult for single genes to win out a competition against the organism – and all other genes – in the long run.

3) Group selection (Population selection) is selection above the level of the individual. Again, many adaptations will benefit both levels (e.g. an improvement of lion's hunting skill is useful on the individual as well as on the group level). Interesting cases arise if there are conflicts. There are many such cases known, and almost always the individual level wins. Examples include many cases of sexual selection. A famous example, already discussed by Darwin, is the peacock's tail. This tail is clearly costly since it handicaps flight and takes resources to grow. It only evolves because females prefer males with a larger tail. Presumably, there was a time when all peacocks had short tails and at this stage it was actually an advantage to have a somewhat longer tail. At this time female preference for long-tailed males was adaptive and evolved. As a consequence, average tail length in males

¹ <http://www.hhmi.org/biointeractive/making-fittest-natural-selection-and-adaptation>

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increased and continued to increase even after the optimal tail length for male viability had been passed. Even at this stage, it is not easy for female choice to switch to a preference for short-tailed males (or even to random mating) since as long as this mutation is rare in the population short tailed sons, even if more viable, will be rejected as males.

In examples like the peacock's the group fitness (the absolute reproductive output of the population – its growth rate) will clearly suffer. In extreme cases individual selection may even drive the group extinct, e.g. if predators reproduce at a rate that offspring overeat the food supply and the whole group starves to death. The important question is whether there are examples where the group level is able to win against the individual level. The common belief among evolutionary biologists is currently that group selection is generally a weak and unimportant process, since both turnover and numbers (opposing genetic drift) are higher at the individual level than at the group level.

Once central topic in the context of group selection where the individual sacrifices part of his fitness for the good of the group is the **evolution of altruism**. The general problem with the evolution of altruism (on the group level) is that altruistic behavior is quickly degraded by selfish spoilers who enjoy the altruism of the other group members but do not pay the cost. Although altruistic groups do better than selfish groups, selection on the group level is a much slower process since groups originate and go extinct at a much slower rate. Since there are many examples of apparent altruistic behavior, this means that adaptive explanations at other levels must be found, e.g. at the individual level through punishment mechanisms for selfish cheaters, reciprocal altruism, spatial structure, etc.).

4) Kin Selection (Family Selection). Many cases of altruistic behavior that seem to require group selection are actually explained by kin selection. Why do mothers invest so much (energy) in their kids although it hurts their own survival? The evolutionary answer is: Because kids carry her genes. She is willing to lower her own chances of survival a bit if it increases her kids' chances of survival. This is easy to understand from a gene point of view: A behavior allele that makes mothers invest a lot of energy in their kids will increase in frequency because copies of the same allele are inherited by the kids, and these copies profit. Conversely, alleles that make mothers not care for their kids may not even make it to the next generation if, as a consequence, all kids die.

Kin selection is a potent mechanism. It works between all kinds of relatives, with decreasing strength depending on the relatedness. Haldane once joked that he would give up his own life for 2 of his brothers or 8 of his cousins. More generally, Hamilton (1964) calculated the conditions under which an "altruistic mutant allele" would spread. His rule reads $rb > c$, where b is benefit of the behavior and c the cost to the altruist. r is the coefficient of relatedness between the altruist and the relative (for identical twins $r = 1$, mother-offspring $r = 1/2$, sibs $r = 1/2$, aunt-niece $r = 1/4$, cousins $r = 1/8$). It measures the probability that 2 alleles drawn at random from altruist and relative are identical. We see that the bigger the cost, the bigger the required relatedness. It is possible to combine the individual and the kin level of selection by adding up direct and indirect fitness effects weighed by relatedness (**inclusive fitness**).

Kinship theory helps explain phenomena that at first sight run counter to the theory of natural selection. For example, many hymenopterans live in large social groups where only a single

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or few females reproduce. All other females protect the queen (e.g. suicidal sacrifice of worker bees) and feed her young offering their lives. At first sight, this behavior seems maladaptive, since it appears that these workers have zero fitness. Hymenopterans are genetically predisposed to evolution of altruism by mean of inclusive fitness due to the special feature of a *haplodiploid* sex determination system. Males develop from unfertilized eggs, are haploid and therefore produce genetically identical sperm. If only one father sires all offspring in a colony the probability of sharing a paternal gene copy is 1. Females develop from fertilized eggs and so are diploid.; the probability of sharing a gene copy via the mother is thus 0.5. This leads to the following average relatedness coefficients:

- e.g. mother with her son/daughter: $r = 0.5$
sister with her sister: $r = 0.5 \times 0.5$ (via mother) + 0.5×1 (via father) = 0.75
sister with her brother: $r = 0.5 \times 0.5$ (via mother) + 0.5×0 (via father) = 0.25
brother with her sister: $r = 1 \times 0.5$ (via mother) = 0.5

Sisters are thus more related to one another than they are to their mothers and fathers! A hymenopteran worker can thus make a greater genetic profit by helping rear a reproductive sister than if she could if she herself would be fertile and produce own offspring. Inclusive fitness may thus help explain the otherwise unintelligible phenomenon of why most females are sterile and only females help rear their sisters. Males are related to their sisters only by 0.5 instead of 0.75 and generally do not get involved in helping.

Adaptation

We have frequently used the term adaptation. We will now define it and discuss some prominent examples. Adaptation is the end product of natural selection: A trait that enables an individual to leave more progeny is called an adaptation (the term “adaptation” is also used to describe the process that leads to this end product).

In general, there are three kinds of traits:

- 1) Traits that are beneficial: true adaptations.
- 2) Traits that are neutral.
- 3) Traits that are deleterious.

The question whether an observed trait is adaptive, and if so, for which reason it evolved is one of the main issues of evolutionary biology. How can we decide whether a trait is a true adaptation? In some cases, adaptation to the environment is so perfect that it is (or seems?) “just obvious” that the trait has been the direct target of natural selection. In this category fall many classic examples of beautiful adaptations, such as crypsis (hide) and mimicry (imitate).

Crypsis. The most famous example is the industrial melanism of *Biston betularia*, the “Peppered moth”: Moths don't like to be seen because they are picked off by birds. Prior to the mid 19th century, woods in England used to be pollution-free and moths were light colored, but pollution during the industrial revolution turned the trees black (esp. in Southern England). In 1848, the first dark moth was found near Manchester; by 1950 or so, 90% of all moths in S. England were dark. After clean-air laws had been enforced, the frequency of dark moths went steeply down again. In 1955, Kettlewell did experiments showing that light moths do better in unpolluted woods, while dark ones do better in polluted woods:

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- 1 He took moths and released them in unpolluted wood (Dorset): 14.6% of lights recaptured, 4.7% of darks recaptured
- 2 He took moths and released them in polluted wood (Manchester): 13.0% of lights recaptured, 27.5% of darks recaptured The “peppered moth story” has recently been criticized since there were doubts whether bird predation is an important selective agent for the moths. However, many evolutionists still think this is the most likely explanation. In any case, there must have been strong selection for the color morph since no other evolutionary force can explain the rapid frequency change that was observed.

Mimicry. The model system for mimicry is butterflies. There are two kinds: 1) In **Batesian mimicry**, the palatable species is protected by resemblance to unpalatable or dangerous species. E.g. birds won't eat the distasteful *Danaus* butterfly (monarch), which is used by the edible mimic *Papilio dardanus*. Batesian mimicry is a form of parasitism. There is selection on the model to move away from the mimic, resulting in a coevolutionary race. 2) In **Müllerian mimicry**, multiple unrelated unpalatable species resemble each other. A predator that ate any won't eat the other. An example are the *Heliconius* butterflies, which all mimic each other. Müllerian mimicry is advantageous for all models; there is thus coevolution to a common phenotype.

Historical dimension

Several authors have argued that a historical dimension is needed to define adaptation. The reason for this claim is that character states, while beneficial, may not have evolved to the purpose it serves today. Darwin recognized this using the example of skull morphology. “The sutures in the skulls of young mammals have been advanced as a beautiful adaptation for aid in parturition, and no doubt they facilitate, or may be indispensable for this act; but as sutures occur in the skulls of young birds and reptiles, which have only to escape from a broken egg, we may infer that this structure has arisen from the laws of growth, and has been taken advantage of in the parturition of the higher animals.” When asking if something is an adaptive trait taking a historical, comparative perspective into account may thus matter. Some features may simply be the result of phylogenetic constraints (a bird with five wings is simply not an option) and not of adaptive evolution. The comparative perspective also helps understand how traits can be co-opted to serve a new function (**exaptation**).

Adaptive “just so” stories

The above cases are good and well-documented examples for adaptations. However, it is remarkably easy to invent an adaptive explanation for almost every feature of phenotype. Without proper testing, this is dangerous and misleading. Traits can be neutral or even deleterious, and even for beneficial traits the adaptive cause why it evolved is often not at all obvious. An example is the giraffe's neck:

The idea that the long necks in giraffes evolved by the need to reach food that is unavailable to other mammals is so plausible that it was commonly accepted among biologists. However, a study in 1996 found that giraffes rarely feed with their necks fully extended, even in the dry season when competition for food should be most severe. This shows that the food competition hypothesis is probably not true. The authors of the study offer a different explanation and back it with data: giraffe bulls use their necks to fight for females and

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observations show that long-necked males have a definite advantage in these fights.

Adaptive stories that are not backed up by experiments are called “just so stories”, after a book by Rudyard Kipling where he gives fantasy explanations of how the leopard got his spots or the camel his hump. In order to avoid this “fantasy trap”, there are two main routes to substantiate the claim:

- a) Direct experiment: paint polar bears black and measure whether survivorship goes down. The release-recapture study that has been done for *Biston betularia* is such a type of experiment.
- b) Indirect by the comparative method: if you think that streamlined shape of fish is an adaptation to moving through fluid, look at other unrelated organisms that face same problem: do squids have the same shape?

Non-Adaptive Traits

There are many ways how characteristics of phenotype can be non-adaptive. Many variants are just neutral (differences are not selectively important). There are many examples from molecular traits: it appears that most nucleotide differences and even protein differences among individuals are neutral.

Maladaptations can happen for a number of reasons. Some occur because there was no better way for evolution to solve the problem (inevitable trade-off of adaptive trait do to historic constraints). Similarly, traits may be maladaptive just because there was not enough time for the “right” mutation to arrive and get selected. A different reason is that genetic drift that may overcome selection in particular in small populations. This explains the spread of many heritable diseases in small, inbred populations.

Literature: (Barton et al. 2007; Futuyma 2013; Nielsen and Slatkin 2013)

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