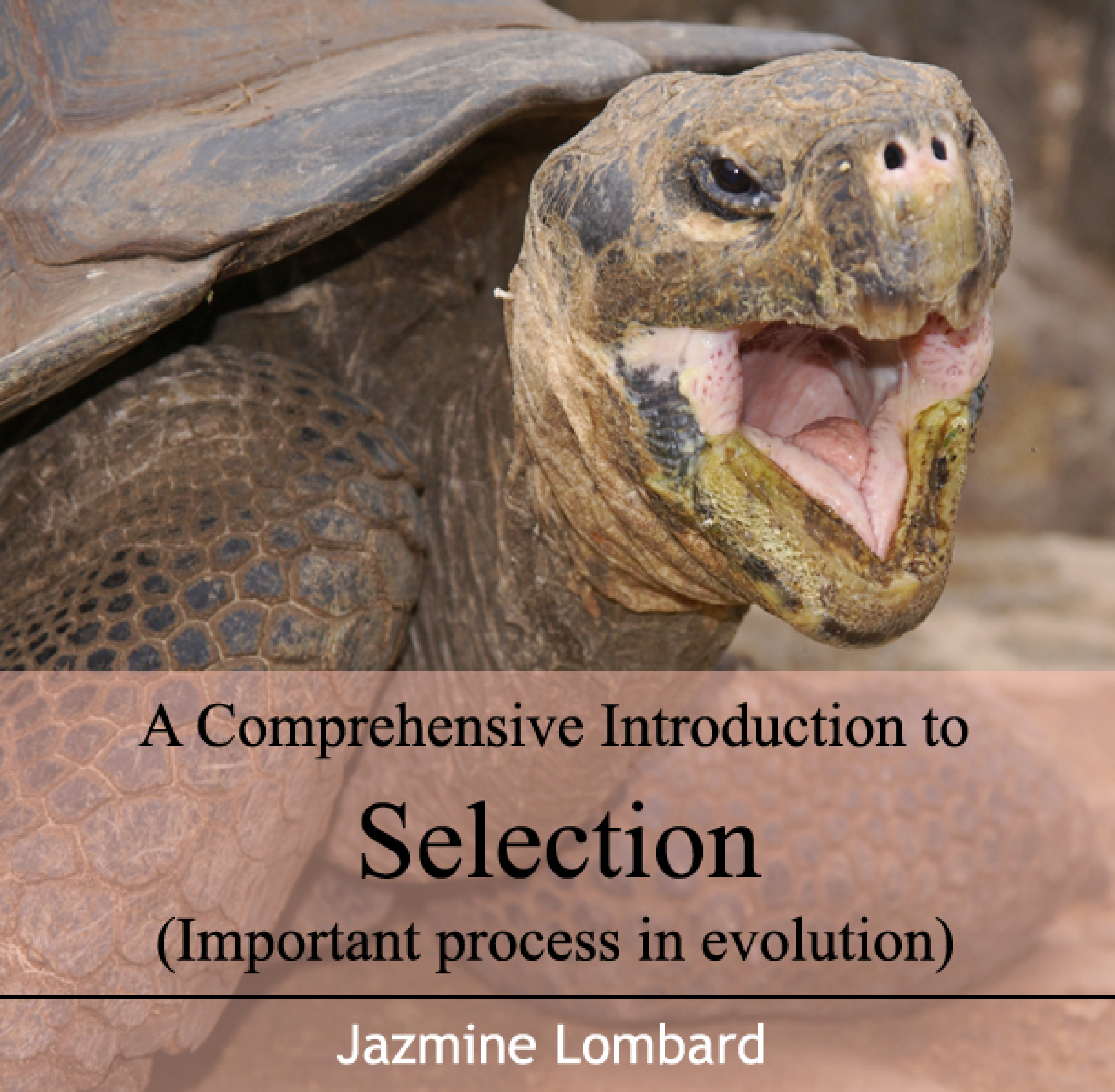

A Comprehensive Introduction to
Selection
(Important process in evolution)

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Introduction

In the context of evolution, certain traits or alleles of genes segregating within a population may be subject to **selection**. Under selection, individuals with advantageous or "adaptive" traits tend to be more successful than their peers reproductively—meaning they contribute more offspring to the succeeding generation than others do. When these traits have a genetic basis, selection can increase the prevalence of those traits, because offspring will inherit those traits from their parents. When selection is intense and persistent, adaptive traits become universal to the population or species, which may then be said to have *evolved*.

Overview

Whether or not selection takes place depends on the conditions in which the individuals of a species find themselves. Adults, juveniles, embryos, and even eggs and sperm may undergo selection. Factors fostering selection include limits on resources (nourishment, habitat space, mates) and the existence of threats (predators, disease, adverse weather). Biologists often refer to such factors as **selective pressures**.

Natural selection is the most familiar type of selection by name. The breeding of dogs, cows and horses, however, represents "artificial selection". Subcategories of natural selection are also sometimes distinguished. These include sexual selection, ecological selection, stabilizing selection, disruptive selection and directional selection (more on these below).

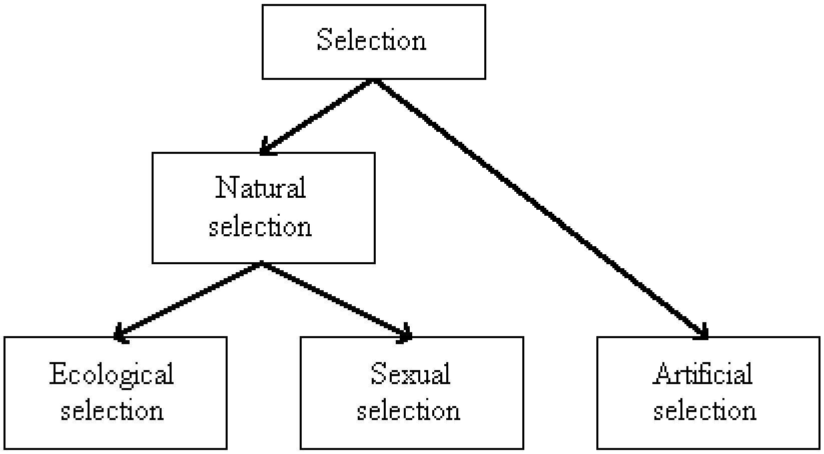
Selection occurs only when the individuals of a population are diverse in their characteristics—or more specifically when the traits of individuals differ with respect to how well they equip them to survive or exploit a particular pressure. In the absence of individual variation, or when variations are **selectively neutral**, selection does not occur.

Meanwhile, selection does not guarantee that advantageous traits or alleles will become prevalent within a population. Through genetic drift, such traits may become less common or disappear. In the face of selection even a so-called *deleterious allele* may become universal to the members of a species. This is a risk primarily in the case of "weak" selection (e.g. an infectious disease with only a low mortality rate) or small populations.

Though deleterious alleles may sometimes become established, selection may act "negatively" as well as "positively." **Negative selection** decreases the prevalence of traits that diminish individuals' capacity to succeed reproductively (i.e. their fitness), while **positive selection** increases the prevalence of adaptive traits.

In biological discussions, traits subject to negative selection are sometimes said to be "selected against," while those under positive selection are said to be "selected for," as in the sentence *Desert conditions select for drought tolerance in plants and select against shallow root architectures.*

Types and subtypes



Selection is hierarchically classified into natural and artificial selection. Natural selection is further subclassified into ecological and sexual selection

Patterns of selection

Aspects of selection may be divided into effects on a phenotype and their causes. The effects are called **patterns of selection**, and do not necessarily result from particular causes (*mechanisms*); in fact each pattern can arise from a number of different mechanisms. Stabilizing selection favors individuals with intermediate characteristics while its opposite, disruptive selection, favors those with extreme characteristics; directional selection occurs when characteristics lie along a phenotypic spectrum and the individuals at one end are more successful; and balancing selection is a pattern in which multiple characteristics may be favored.

Mechanisms of selection

Distinct from patterns of selection are **mechanisms of selection**; for example, disruptive selection often is the result of disassortative sexual selection, and balancing selection may result from frequency-dependent selection and overdominance.

Chapter- 1

Balancing Selection

Balancing selection refers to a number of selective processes by which multiple alleles (different versions of a gene) are actively maintained in the gene pool of a population *at frequencies above that of gene mutation*. This usually happens when the heterozygotes for the alleles under consideration have a higher adaptive value than the homozygote. In this way genetic polymorphism is conserved.

Biston betularia morpha *typica*, the standard light-coloured Peppered Moth.

Biston betularia morpha *carbonaria*, the melanic Peppered Moth. The proportions of this form vary in different locations

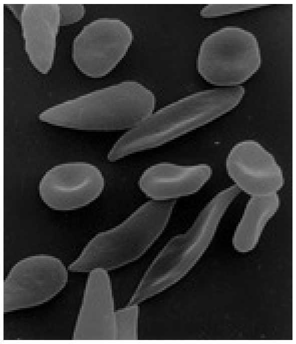
There are three main types of natural selection: In directional selection the allele frequency for a trait continuously shifts in one direction. In stabilizing selection the frequency of the alleles of lower fitness decreases until they vanish. Balancing selection is similar but not identical to disruptive selection where individuals of extreme trait values are favored against those with average trait values. These terms are used for quantitative characters controlled by a number of genes.

Evidence for balancing selection can be found in the number of alleles in a population which are maintained above mutation rate frequencies. All modern research has shown that this significant genetic variation is ubiquitous in panmictic populations. It is a genetic expression of the field experience of Darwin, Wallace and others, that natural populations in the wild are extraordinarily varied (though not all such variation is of genetic origin).

There are several mechanisms (which are not exclusive within any given population) by which balancing selection works to maintain polymorphism. The two major and most studied are *heterozygote advantage* and *frequency-dependent selection*.

Mechanisms of balancing selection

Heterozygote advantage



Sickle-shaped red blood cells. This non-lethal condition in heterozygotes is maintained by balancing selection in humans of Africa and India due to its resistance to the malarial parasite.

In heterozygote advantage, or *heterotic balancing selection*, an individual who is heterozygous at a particular gene locus has a greater fitness than a homozygous individual. Polymorphisms maintained by this mechanism are *balanced polymorphisms*.

A well-studied case is that of sickle cell anemia in humans, a hereditary disease that damages red blood cells. Sickle cell anemia is caused by the inheritance of a variant hemoglobin gene (HgbS) from both parents. In these individuals, hemoglobin in red blood cells is extremely sensitive to oxygen deprivation, and this causes shorter life expectancy. A person who inherits the sickle cell gene from one parent, and a normal hemoglobin gene (HgbA) from the other, has a normal life expectancy. However, these heterozygote individuals, known as *carriers* of the sickle cell trait, may suffer problems from time to time.

The heterozygote is resistant to the malarial parasite which kills a large number of people each year. This is balancing selection between fierce selection against homozygous sickle-cell sufferers, and selection against the standard HgbA homozygotes by malaria. The heterozygote has a permanent advantage (a higher fitness) wherever malaria exists.

Frequency-dependent selection

Frequency-dependent selection occurs when the fitness of a phenotype is dependent on its frequency relative to other phenotypes in a given population. In *positive frequency-dependent selection* the fitness of a phenotype increases as it becomes more common. In *negative frequency-dependent selection* the fitness of a phenotype increases as it becomes less common. For example in prey switching, rare morphs of prey are actually fitter due to predators concentrating on the more frequent morphs.

Fitness varies in time & space

The fitness of a genotype may vary greatly between larval and adult stages, or between parts of a habitat range.

Selection acts at different levels

The fitness of a genotype may depend on the fitness of other genotypes in the population: this covers many natural situations where the best thing to do (from the point of view of survival and reproduction) depends on what other members of the population are doing at the time.

More complex examples

Species in their natural habitat are often far more complex than the typical text-book examples.

Grove snail

The Grove Snail, *Cepaea nemoralis*, is famous for the rich polymorphism of its shell. The system is controlled by a series of multiple alleles. Unbanded is the top dominant trait, and the forms of banding are controlled by modifier genes.

Grove snail, dark yellow shell with single band.

In England the snail is regularly preyed upon by the Song Thrush *Turdus philomelos*, which breaks them open on *thrush anvils* (large stones). Here fragments accumulate, permitting researchers to analyse the snails taken. The thrushes hunt by sight, and capture selectively those forms which match the habitat *least well*. Snail colonies are found in woodland, hedgerows and grassland, and the predation determines the proportion of phenotypes (morphs) found in each colony.

Two active Grove snails

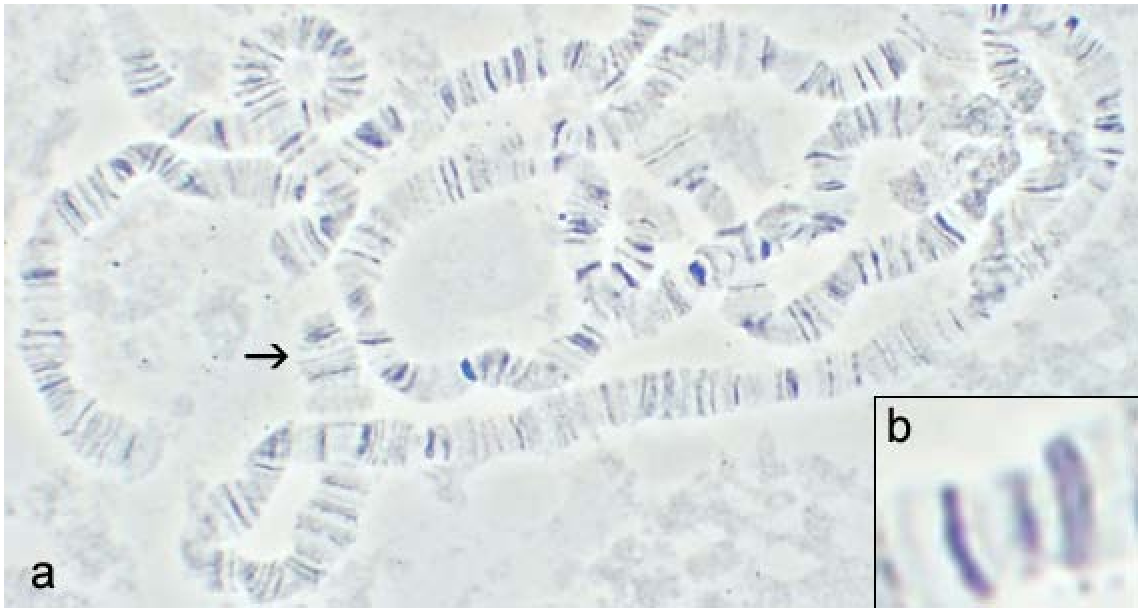
A second kind of selection also operates on the snail, whereby certain heterozygotes have a physiological advantage over the homozygotes. Thirdly, apostatic selection is likely, with the birds preferentially taking the most common morph. This is the 'search pattern' effect, where a predominantly visual predator persists in targeting the morph which gave a good result, even though other morphs are available.

The polymorphism survives in almost all habitats, though the proportions of morphs varies considerably. The alleles controlling the polymorphism form a super-gene with linkage so close as to be nearly absolute. This control saves the population from a high proportion of undesirable recombinants.

To sum up, in this species predation by birds appears to be the main (but not the only) selective force driving the polymorphism. The snails live on heterogeneous backgrounds, and thrush are adept at detecting poor matches. The inheritance of physiological and cryptic diversity is preserved also by heterozygous advantage in the super-gene. Recent work has included the effect of shell colour on thermoregulation, and a wider selection of possible genetic influences is considered by Cook.

Chromosome polymorphism in *Drosophila*

In the 1930s Dobzhansky and his co-workers collected *Drosophila pseudoobscura* and *D. persimilis* from wild populations in California and neighbouring states. Using Painter's technique they studied the polytene chromosomes and discovered that all the wild populations were polymorphic for chromosomal inversions. All the flies look alike whatever inversions they carry, so this is an example of a cryptic polymorphism. Evidence accumulated to show that natural selection was responsible:



Drosophila polytene chromosome

1. Values for heterozygote inversions of the third chromosome were often much higher than they should be under the null assumption: if no advantage for any form the number of heterozygotes should conform to N_s (number in sample) = $p^2+2pq+q^2$ where 2pq is the number of heterozygotes.

2. Using a method invented by L'Heretier and Teissier, Dobzhansky bred populations in *population cages*, which enabled feeding, breeding and sampling whilst preventing escape. This had the benefit of eliminating migration as a possible explanation of the results. Stocks containing inversions at a known initial frequency can be maintained in controlled conditions. It was found that the various chromosome types do not fluctuate at random, as they would if selectively neutral, but adjust to certain frequencies at which they become stabilised.

3. Different proportions of chromosome morphs were found in different areas. There is, for example, a polymorph-ratio cline in *D. robusta* along an 18-mile (29 km) transect near Gatlinburg, TN passing from 1,000 feet (300 m) to 4,000 feet. Also, the same areas sampled at different times of year yielded significant differences in the proportions of forms. This indicates a regular cycle of changes which adjust the population to the seasonal conditions. For these results selection is by far the most likely explanation.

4. Lastly, morphs cannot be maintained at the high levels found simply by mutation, nor is drift a possible explanation when population numbers are high.

By 1951 Dobzhansky was persuaded that the chromosome morphs were being maintained in the population by the selective advantage of the heterozygotes, as with most polymorphisms.

Chapter- 2

Group Selection

In evolutionary biology, **group selection** refers to the idea that alleles can become fixed or spread in a population because of the benefits they bestow on groups, regardless of the alleles' effect on the fitness of individuals within that group.

Group selection was used as a popular explanation for adaptations, especially by V. C. Wynne-Edwards. For several decades, however, critiques, particularly by George C. Williams,John Maynard Smith and C.M. Perrins (1964), cast serious doubt on group selection as a major mechanism of evolution, and though some scientists have pursued the idea over the last few decades, only recently have group selection models seen a minor resurgence (albeit not as a fundamental mechanism but as a phenomenon emergent from standard selection).

Overview

Specific syndromes of selective factors can create situations where groups are selected because they display group properties that are selected-for. Some mosquito-transmitted rabbit viruses, for instance, are only transmitted to uninfected rabbits from infected rabbits that are still alive. This creates a selective pressure on every group of viruses already infecting a rabbit not to become too virulent and kill their host rabbit before enough mosquitoes have bitten it. In natural systems such viruses display much lower virulence levels than do mutants of the same viruses that in laboratory culture readily out-compete non-virulent variants (or than do tick-transmitted viruses—ticks, unlike mosquitoes, bite dead rabbits).

However, theoretical models of the 1960s seemed to imply that the effect of group selection was negligible. Alleles are likely to be held on a population-wide level, leaving nothing for group selection to select for. Additionally, generation time is much longer for groups than it is for individuals. Assuming conflicting selection pressures, individual selection will occur much faster, swamping any changes potentially favored by group selection. The Price equation can partition variance caused by natural selection at the individual level and the group level, and individual level selection generally causes greater effects.

Experimental results starting in the late 1970s demonstrated that group selection was far more effective than the then-current theoretical models had predicted. A review of this experimental work has shown that the early group selection models were flawed because they assumed that genes acted independently, whereas in the experimental work it was apparent that gene interaction, and more importantly, genetically based interactions among individuals, were an important source of the response to group selection (e.g.). As a result many are beginning to recognize that group selection, or more appropriately multilevel selection, is potentially an important force in evolution.

More recently, Yaneer Bar-Yam has claimed that the gene-centered view (and thus Ronald Fisher's treatment of evolution) relies upon a mathematical approximation that is not generally valid. Bar-Yam argues that the approximation is a dynamic form of the Mean Field approximation frequently used in physics and whose limitations are recognized there. In biology, the approximation breaks down when there are spatial populations resulting in inhomogeneous genetic types (called symmetry breaking in physics). Such symmetry breaking may also correspond to speciation.

Spatial populations of predators and prey have also been shown to show restraint of reproduction at equilibrium, both individually and through social communication, as originally proposed by Wynne-Edwards. While these spatial populations do not have well-defined groups for group selection, the local spatial interactions of organisms in transient groups are sufficient to lead to a kind of multi-level selection. There is however as yet no evidence that these processes operate in the situations where Wynne-Edwards posited them; Rauch et al.'s analysis, for example, is of a host-parasite situation, which was recognised as one where group selection was possible even by E. O. Wilson (1975), in a treatise broadly hostile to the whole idea of group selection. Specifically, the parasites do not individually moderate their transmission; rather, more transmissible variants "continually arise and grow rapidly for many generations but eventually go extinct before dominating the system."

The haystack model and trait groups

Maynard Smith can be credited with what has become known as the "haystack model" of group selection. As a non-mathematical introduction to the idea, imagine a group of animals that spend most of their time living and breeding in haystacks but that occasionally all come out of their haystacks simultaneously, mix together and then separate into equal groups, which once again go off to inhabit separate haystacks. We can then imagine a trait that benefits each haystack group, perhaps leading to behaviorally altruistic acts that cost an individual some fitness but enhance the fitness of its group even more, and a selfish trait that, for the purposes of this discussion, we can call the absence of the altruistic trait.

Each of these two traits works on a different level of selection. Within the individual haystacks the selfish organisms benefit in terms of evolutionary fitness. This is because the selfish organisms benefit from the actions of the altruistic organisms but do not pay any of the evolutionary costs for being altruistic (sacrificing some good for that of others). Thus, in each generation the number of altruists in the group would shrink compared to the number of selfish organisms. As a result one might first think that a group beneficial trait, especially an altruistic one, would be doomed to eventually die out. But we must remember the strange nature of these hypothetical organisms. Every so often, at the same time, all the members of all the haystacks form one large group, randomly assort into equal groups, and then move back into the haystacks. Because of this an altruistic behavior can take hold by the following reasoning. While the number of selfish organisms in each haystack increases in percentage every generation, the total population of haystacks that contain altruists produce more offspring over all than those that do not. This means that populations with altruists are going to be over-represented when all the haystacks are abandoned to form a larger group. So long as the number of generations spent in each haystack is not so long as to dramatically reduce the number of altruists, and so long as the group benefit of the altruistic trait is significant enough, the number of altruists in all the haystack populations can rise.

However, though Maynard Smith gave a mathematical model by which group selection might work, he was skeptical that it would happen in nature often enough to be worth considering. His reasoning was that the specific conditions for group selection to take hold, namely the repeated isolation, mixture, and reisolation of organisms would be so rare and unlikely to occur in nature that it was almost certainly not a significant evolutionary force.

In their 1998 book *Unto Others*, and in various articles before this, Sober and David Sloan Wilson challenge this view. While one of their challenges takes the form of naming organisms, such as the so called "brain worm" (*Dicrocoelium dendriticum*), which has a life cycle much like that of the haystack organisms above, they present a more significant argument, based on the notion of trait groups.

Trait groups can occur within larger groups through the interaction of particular genetic traits, and need not interact for a generation to promote survival value. Sober and Wilson see kin selection, which is often considered an alternative to group selection, as a special case of a trait groups. To see how a trait group could be beneficial, let's imagine an altruist trait, such as cooperation with another organism even in such cases were it only benefits 40% as much as the organism it helps, and a selfish trait such as cooperating with another organism only when it will benefit more than the organism it helps. The first trait is considered altruistic in Sober and Wilson’s sense because the within-group fitness of the altruistic organism drops every time it cooperates compared with the other member of the group. Now imagine five organisms, one of which is altruistic in regards to this trait, and the rest of which are selfish. Assume that each case of cooperation increases the chance of survival and reproduction by 10 units, which is divided among the interacting pair (group of two). Now assume that member of the population groups/interacts with each other member of the population one time. After all the interactions have taken place, the selfish organisms have each acquired 6 units. This is because they all refuse to cooperation with other selfish members (since it is impossible for both members to benefit more than the other), but each takes advantage of the altruist benefits over that individual in a ratio of 60% to 40%. The altruist on the other hand has interacted with 4 selfish organisms and thus has earned 16 units (four for each encounter) and thus has a greater survival advantage than the selfish members of the population. The altruist ends up winning the survival "war" even though it came out behind in every survival "battle".

Because individuals can form hundreds or even thousands of trait groups within its life span, the trait group selection model does not have to rely on the unlikely situation of an entire population isolating into groups, merging, and then isolating into groups again. Likewise the rate at which trait groups can form and dissolve can be many times faster than the rate at which individuals reproduce, providing cumulative as opposed to all-or-nothing benefits. It is important to note that this argument has not settled the issue of group selection however. There is still heavy debate as to whether or not such formations count as “real” groups in the traditional biological sense of groups affected by group selection.

Multilevel selection theory

In recent years, the limitations of earlier models have been addressed, and newer models suggest that selection may sometimes act above the gene level. Recently David Sloan Wilson and Elliot Sober have argued that the case against group selection has been overstated. They focus their argument on whether groups can have functional organization in the same way individuals do and, consequently, whether groups can also be "vehicles" for selection. For example, groups that cooperate better may have out-reproduced those that did not. Resurrected in this way, Wilson & Sober's new group selection is usually called multilevel selection theory.

David Sloan Wilson, the developer of Multilevel Selection Theory (MLS) compares the many layers of competition and evolution to the “Russian Matryoska Dolls” within one another. The lowest level is the genes, next come the cells, and then the organism level and finally the groups. The different levels function cohesively to maximize fitness, or reproductive success. After establishing these levels, MLS goes further by saying that selection for the group level, which is competition between groups, must outweigh the individual level, which is individuals competing within a group, for a group-beneficiating trait to spread. MLS theory focuses on the phenotype this way because it looks at the levels that selection directly acts upon.

MLS theory is not leaning towards individual or group selection but can be used to evaluate the balance between group selection and individual selection on a case-by-case scenario. It serves as middle ground for the extreme theories of kin selection or individual selection. Some experiments done imply that group selection can prevail, such as the experiment conducted by William Muir of Purdue University comparing egg productivity in hens. In the experiment, he demonstrates the existence of group selection by showing that in individual selection, a hyper-aggressive strain had been produced that led to many fatal attacks only after six generations. Group selection has been most often postulated in humans and, notably, social insects that make cooperation a driving force of their adaptations over time.

For humans, a highly pro-social, cognitive thinking species, social norms can be seen as a means of reducing the individual level variation and competition and shift selection in humans to the group level. Wilson ties the MLS theory regarding humans to another upcoming theory known as gene-culture evolution by acknowledging that culture seems to characterize a group-level mechanism for human groups to adapt to environmental changes. The ways to test MLS is through social psychological experimentation and multilevel modeling equations.

Although Richard Dawkins and fellow advocates of the gene-centered view of evolution remain unconvinced, Wilson & Sober's work has been part of a broad revival of interest in multilevel selection as an explanation for evolutionary phenomena. Indeed, in a 2005 article, E. O. Wilson argued that kin selection could no longer be thought of as underlying the evolution of extreme sociality, for two reasons. First, some authors have shown that the argument that haplodiploid inheritance, characteristic of the Hymenoptera, creates a strong selection pressure towards nonreproductive castes is mathematically flawed. Second, eusociality no longer seems to be confined to the hymenopterans; increasing numbers of highly social taxa have been found in the years since Wilson's foundational text on sociobiology was published in 1975, including a variety of insect species, as well as a rodent species (the naked mole rat). Wilson suggests the equation for Hamilton's rule:

$$rb > c$$

(where b represents the benefit to the recipient of altruism, c the cost to the altruist, and r their degree of relatedness) should be replaced by the more general equation

$$(rb_k + b_e) > c$$

in which b_k is the benefit to kin (b in the original equation) and b_e is the benefit accruing to the group as a whole. He then argues that, in the present state of the evidence in relation to social insects, it appears that $b_e >> rb_k$, so that altruism needs to be explained in terms of selection at the colony level rather than at the kin level. However, it is well understood in social evolution theory that kin selection and group selection are not distinct processes, and that the effects of multi-level selection are already fully accounted for in Hamilton's original rule, $rb>c$.

Group selection indicated by gene-culture coevolution

Gene-culture coevolution is a modern hypothesis (applicable mostly to humans) that combines evolutionary biology and modern sociobiology to indicate group selection. It treats culture as a separate evolutionary system that acts in parallel to the usual genetic evolution to transform human traits. It is believed that this approach of combining genetic influence with cultural influence over several generations is not present in the other hypotheses such as reciprocal altruism and kin selection, making gene-culture evolution one of the strongest realistic hypotheses for group selection. Fehr provides evidence of group selection taking place in humans presently with experimentation through logic games such as prisoner’s dilemma, the type of thinking that humans have developed many generations ago.

Gene-culture coevolution, or cumulative cultural evolution, allows humans to culturally evolve highly distinct adaptations to the local pressures and environments much quicker than with genetic evolution alone. Robert Boyd and Peter J. Richerson, two strong proponents of cultural evolution, postulate that the act of social learning, or learning in a group as done in group selection, allows human populations to accrue information over many generations. This leads to the cultural evolution of highly adaptive behaviors and technology alongside genetic evolution. Specifically, they believe that the ability to collaborate with each other evolved during the Middle Pleistocene, a million years ago, in response to a rapidly-changing climate.

Herbert Gintis approaches cultural evolution of group selection in a much more statistical approach to prove that societies that promote pro-social norms, as in group selection, have higher survival rates than societies that do not. He does so by developing a multilevel gene-culture coevolutionary model that explains the process whereby altruistic social norms will hinder socially harmful and fitness reducing norms and consequently will be internalized. In his equations, he differentiates between a genetic group selection model that is sensitive to group size and migration rates versus his own model that is much less affected by these constraints and therefore more accurate.

Group selection due to differing ESSs

The problem with group selection is that for a whole group to get a single trait, it must spread through the whole group first by regular evolution. But, as J. L. Mackie suggested, when there are many different groups, each with a different Evolutionarily Stable Strategy (ESS), there is selection between the different ESSs, since some are worse than others. For example, a group where altruism arose would outcompete a group where every creature acted in its own interest.

Chapter- 3

Kin Selection

Kin selection refers to apparent strategies in evolution that favor the reproductive success of an organism's relatives, even at a cost to their own survival and/or reproduction. The classic example is a eusocial insect colony, in which sterile females act as workers to assist their mother in the production of additional offspring.

The earliest expressions of the basic concepts were by R.A. Fisher in 1930, J. B. S. Haldane in 1955, but it was W. D. Hamilton who truly formalized the concept, in works published in 1963 and—most importantly—in 1964. The term "kin selection" may first have been coined by John Maynard Smith in 1964 when he wrote:

These processes I will call kin selection and group selection respectively. Kin selection has been discussed by Haldane and by Hamilton. … By kin selection I mean the evolution of characteristics which favour the survival of close relatives of the affected individual, by processes which do not require any discontinuities in the population breeding structure.

Kin selection refers to changes in gene frequency across generations that are driven at least in part by interactions between related individuals, and this forms much of the conceptual basis of the theory of social evolution. Indeed, some cases of evolution by natural selection can only be understood by considering how biological relatives influence one another's fitness. Under natural selection, a gene encoding a trait that enhances the fitness of each individual carrying it should increase in frequency within the population; and conversely, a gene that lowers the individual fitness of its carriers should be eliminated. However, a hypothetical gene that prompts behaviour which enhances the fitness of relatives but lowers that of the individual displaying the behavior, may nonetheless increase in frequency, because relatives often carry the same gene; this is the fundamental principle behind the theory of kin selection. According to the theory, the enhanced fitness of relatives can at times more than compensate for the fitness loss incurred by the individuals displaying the behaviour. As such, this is a special case of a more general model, called inclusive fitness (in that inclusive fitness refers simply to gene copies in other individuals, without requiring that they be kin). However the validity of this analysis has recently been challenged

Hamilton's rule

Formally, such genes should increase in frequency when

$$rB > C$$

where

> *r* = the genetic relatedness of the recipient to the actor, often defined as the probability that a gene picked randomly from each at the same locus is identical by descent.
> *B* = the additional reproductive benefit gained by the recipient of the altruistic act,
> *C* = the reproductive cost to the individual of performing the act.

This inequality is known as **Hamilton's rule** after W. D. Hamilton who published, in 1964, the first formal quantitative treatment of kin selection to deal with the evolution of apparently altruistic acts. Altruistic acts are those that benefit the recipient but harm the actor. The phrase **Kin selection**, however, was coined by John Maynard Smith.

Originally, the definition for relatedness (r) in Hamilton's rule was explicitly given as Sewall Wright's coefficient of relationship: the probability that at a random locus, the alleles there will be identical by descent (Hamilton 1963, American Naturalist, p. 355). Subsequent authors, including Hamilton, sometimes reformulate this with a regression, which, unlike probabilities, can be negative, and so it is possible for individuals to be negatively related, which simply means that two individuals can be less genetically alike than two random ones on average (Hamilton 1970, Nature & Grafen 1985 Oxford Surveys in Evolutionary Biology). This has been invoked to explain the evolution of spiteful behaviours. Spiteful behavior defines an act (or acts) that results in harm, or loss of fitness, to both the actor and the recipient.

In the 1930s J.B.S. Haldane had full grasp of the basic quantities and considerations that play a role in kin selection. He famously said that, "I would lay down my life for two brothers or eight cousins". **Kin altruism** is the term for altruistic behaviour whose evolution is supposed to have been driven by kin selection.

Haldane's remark alluded to the fact that if an individual loses its life to save two siblings, four nephews, or eight cousins, it is a "fair deal" in evolutionary terms, as siblings are on average 50% identical by descent, nephews 25%, and cousins 12.5% (in a diploid population that is randomly mating and previously outbred). But Haldane also joked that he would truly die only to save more than a single identical twin of his or more than two full siblings.

Mechanisms

An altruistic case is one where the instigating individual suffers a fitness loss while the receiving individual benefits by a fitness gain. The sacrifice of one individual to help another is an example of altruism.

Hamilton (1964) outlined two ways in which kin selection altruism could be favoured.

Kin Recognition: Firstly, if individuals have the capacity to recognize kin (kin recognition) and to adjust their behaviour on the basis of kinship (kin discrimination), then the average relatedness of the recipients of altruism could be high enough for this to be favoured. Because of the facultative nature of this mechanism, it is generally regarded that kin recognition and discrimination are unimportant except among 'higher' forms of life (although there is some evidence for this mechanism among protozoa). A special case of the kin recognition/discrimination mechanism is the hypothetical 'green beard', where a gene for social behaviour also causes a distinctive phenotype that can be recognised by other carriers of the gene. Hamilton's discussion of greenbeard altruism serves as an illustration that relatedness is a matter of genetic similarity and that this similarity is not necessarily caused by genealogical closeness (kinship).

Viscous Populations: Secondly, even indiscriminate altruism may be favoured in so-called viscous populations, i.e. those characterized by low rates or short ranges of dispersal. Here, social partners are typically genealogically-close kin, and so altruism may be able to flourish even in the absence of kin recognition and kin discrimination faculties—spatial proximity serves as a rudimentary form of discrimination. This suggests a rather general explanation for altruism. Directional selection will always favor those with higher rates of fecundity within a certain population. Social individuals can often ensure the survival of their own kin by participating in, and following the rules of a group (assuming the implied faculties for group discrimination).

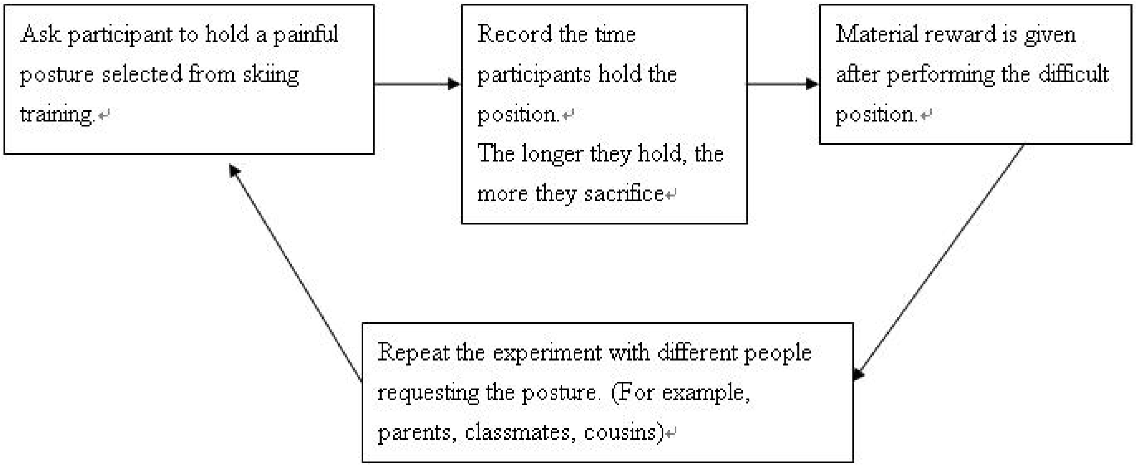
These mechanisms explain a relatively high r between interacting individuals. Absolute genetic similarity is not a measure of r; rather, r shows the “excess” relatedness between an actor and a recipient compared with the relatedness between an actor and a random member of the population. Thus, in a clonal population with 100% genetic similarity, $r = 0$ (as strange as that may sound). This is because there can be no correlation between genetic similarity and interaction strengths if genetic similarity is constant.

It has often been observed that altruism cannot be maintained in a population of randomly interacting individuals. In such a population, the correlation between genetic similarity and interaction strength is necessarily absent, thus $r = 0$ and $rB < C$ for any $C > 0$. This is why mechanisms such as spatial structure and kin recognition are so important for the long-term stability of altruistic traits, and why measures such as "population-wide average r" are meaningless in the absence of such mechanisms.

Kin Selection in evolutionary psychology

Evolutionary psychologists have attempted to explain prosocial behavior through kin selection by stating that “behaviors that help a genetic relative are favored by natural selection.” Human beings have developed a tendency over time to frame and interpret their actions as an avenue to the survival of their genetic material, making kin selection not a completely altruistic form of prosocial behavior and is perhaps better described as a component of social exchange theory. This theory does not necessarily imply that people “compute” genetic benefit when helping others, but there is an indication that those who behave in such a way are more likely to pass on their genes to future generations.

Examples



Ask participant to hold a painful posture selected from skiing training.↵

Record the time participants hold the position.↵
The longer they hold, the more they sacrifice↵

Material reward is given after performing the difficult position.↵

Repeat the experiment with different people requesting the posture. (For example, parents, classmates, cousins)↵

Experiment about Kin Selection

Eusociality (true sociality) is used to describe social systems with three characteristics: one is an overlap in generations between parents and their offspring, two is cooperative brood care, and the third characteristic is specialized castes of nonreproductive individuals. Social insects are an excellent example of organisms that display presumed kin selected traits. The workers of some species are sterile, a trait that would not occur if individual selection was the only process at work. The relatedness coefficient *r* is abnormally high between the worker sisters in a colony of Hymenoptera due to haplodiploidy, and Hamilton's rule is presumed to be satisfied because the benefits in fitness for the workers are believed to exceed the costs in terms of lost reproductive opportunity, though this has never been demonstrated empirically. There are competing hypotheses, as well, which may also explain the evolution of social behavior in such organisms.

Alarm calls in ground squirrels are another example. While they may alert others of the same species to danger, they draw attention to the caller and expose it to increased risk of predation. Paul Sherman, of Cornell University, studied the alarm calls of ground squirrels. He observed that they occurred most frequently when the caller had relatives nearby. In a similar study, John Hoogland was able to follow individual males through different stages of life. He found that the male prairie dogs modified their rate of calling when closer to kin. These behaviors show that self-sacrifice is directed towards close relatives and that there is an indirect fitness gain.

Alan Krakauer of University of California, Berkeley has studied kin selection in the courtship behavior of wild turkeys. Like a teenager helping her older sister prepare for prom night, a subordinate turkey may help his dominant brother put on an impressive team display that is only of direct benefit to the dominant member.

Recent studies provide evidence that even certain plants can recognize and respond to kinship ties. Using sea rocket for her experiments, Susan Dudley at McMaster University in Canada compared the growth patterns of unrelated plants sharing a pot to plants from the same clone. She found that unrelated plants competed for soil nutrients by aggressive root growth. This did not occur with sibling plants.

In human fertilization, some sperm cells consume their acrosome prematurely on the surface of the egg cell, facilitating for surrounding sperms, having on average 50% genome similarity, to penetrate the egg cell.

In the wood mouse (*Apodemus sylvaticus*), aggregates of spermatozoa form mobile trains, some of the spermatozoa undergo a premature acrosome reactions that correlate to improved mobility of the mobile trains towards the female egg for fertilization. This association is thought to proceed as a result of a "green beard effect" in which the spermatozoa perform a kin-selective altruistic act after identifying genetic similarity with the surrounding spermatozoa.

The theory of Kin selection has had a profound impact on interpretations of genetic evolution of eusociality but it has been recently criticized by Martin Nowak and EO Wilson, striking a blow in an increasingly heated debate about evolution of eusociality. The authors argue that "Inclusive fitness theory is not a simplification over the standard approach. It is an alternative accounting method, but one that works only in a very limited domain. Whenever inclusive fitness does work, the results are identical to those of the standard approach. Inclusive fitness theory is an unnecessary detour, which does not provide additional insight or information."

Chapter- 4

Natural Selection

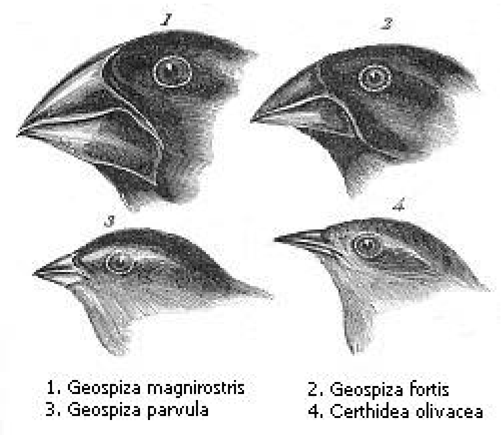
Natural selection is the process by which traits become more or less common in a population due to consistent effects upon the survival or reproduction of their bearers. It is a key mechanism of evolution.

The natural genetic variation within a population of organisms may cause some individuals to survive and reproduce more successfully than others in their current environment. For example, the peppered moth exists in both light and dark colours in the United Kingdom, but during the industrial revolution many of the trees on which the moths rested became blackened by soot, giving the dark-colored moths an advantage in hiding from predators. This gave dark-colored moths a better chance of surviving to produce dark-colored offspring, and in just a few generations the majority of the moths were dark. Factors which affect reproductive success are also important, an issue which Charles Darwin developed in his ideas on sexual selection.

Natural selection acts on the phenotype, or the observable characteristics of an organism, but the genetic (heritable) basis of any phenotype which gives a reproductive advantage will become more common in a population. Over time, this process can result in adaptations that specialize populations for particular ecological niches and may eventually result in the emergence of new species. In other words, natural selection is an important process (though not the only process) by which evolution takes place within a population of organisms. As opposed to artificial selection, in which humans favor specific traits, in natural selection the environment acts as a sieve through which only certain variations can pass.

Natural selection is one of the cornerstones of modern biology. The term was introduced by Darwin in his influential 1859 book *On the Origin of Species*, in which natural selection was described as analogous to artificial selection, a process by which animals and plants with traits considered desirable by human breeders are systematically favored for reproduction. The concept of natural selection was originally developed in the absence of a valid theory of heredity; at the time of Darwin's writing, nothing was known of modern genetics. The union of traditional Darwinian evolution with subsequent discoveries in classical and molecular genetics is termed the *modern evolutionary synthesis*. Natural selection remains the primary explanation for adaptive evolution.

General principles



Finches from Galapagos Archipelago

Darwin's illustrations of beak variation in the finches of the Galápagos Islands, which hold 13 closely related species that differ most markedly in the shape of their beaks. The beak of each species is suited to its preferred food, suggesting that beak shapes evolved by natural selection.

Natural variation occurs among the individuals of any population of organisms. Many of these differences do not affect survival (such as differences in eye color in humans), but some differences may improve the chances of survival of a particular individual. A rabbit that runs faster than others may be more likely to escape from predators, and algae that are more efficient at extracting energy from sunlight will grow faster. Something that increases an animal's survival will often also include its reproductive rate; however, sometimes there is a trade-off between survival and current reproduction. Ultimately, what matters is total lifetime reproduction of the animal.

If the traits that give these individuals a reproductive advantage are also heritable, that is, passed from parent to child, then there will be a slightly higher proportion of fast rabbits or efficient algae in the next generation. This is known as *differential reproduction*. Even if the reproductive advantage is very slight, over many generations any heritable advantage will become dominant in the population. In this way the natural environment of an organism "selects" for traits that confer a reproductive advantage, causing gradual changes or evolution of life. This effect was first described and named by Charles Darwin.

The concept of natural selection predates the understanding of genetics, the mechanism of heredity for all known life forms. In modern terms, selection acts on an organism's phenotype, or observable characteristics, but it is the organism's genetic make-up or genotype that is inherited. The phenotype is the result of the genotype and the environment in which the organism lives.

This is the link between natural selection and genetics, as described in the modern evolutionary synthesis. Although a complete theory of evolution also requires an account of how genetic variation arises in the first place (such as by mutation and sexual reproduction) and includes other evolutionary mechanisms (such as genetic drift and gene flow), natural selection appears to be the most important mechanism for creating complex adaptations in nature.

Nomenclature and usage

The term *natural selection* has slightly different definitions in different contexts. It is most often defined to operate on heritable traits, because these are the traits that directly participate in evolution. However, natural selection is "blind" in the sense that changes in phenotype (physical and behavioral characteristics) can give a reproductive advantage regardless of whether or not the trait is heritable (non heritable traits can be the result of environmental factors or the life experience of the organism).

Following Darwin's primary usage the term is often used to refer to both the evolutionary consequence of blind selection and to its mechanisms. It is sometimes helpful to explicitly distinguish between selection's mechanisms and its effects; when this distinction is important, scientists define "natural selection" specifically as "those mechanisms that contribute to the selection of individuals that reproduce", without regard to whether the basis of the selection is heritable. This is sometimes referred to as "phenotypic natural selection".

Traits that cause greater reproductive success of an organism are said to be selected for, whereas those that reduce success are selected against. Selection for a trait may also result in the selection of other correlated traits that do not themselves directly influence reproductive advantage. This may occur as a result of pleiotropy or gene linkage.

Fitness

The concept of fitness is central to natural selection. Broadly, individuals which are more "fit" have better potential for survival, as in the well-known phrase "survival of the fittest". However, as with natural selection above, the precise meaning of the term is much more subtle, and Richard Dawkins manages in his later books to avoid it entirely. (He devotes a chapter of his book, *The Extended Phenotype*, to discussing the various senses in which the term is used). Modern evolutionary theory defines fitness not by how long an organism lives, but by how successful it is at reproducing. If an organism lives half as long as others of its species, but has twice as many offspring surviving to adulthood, its genes will become more common in the adult population of the next generation.

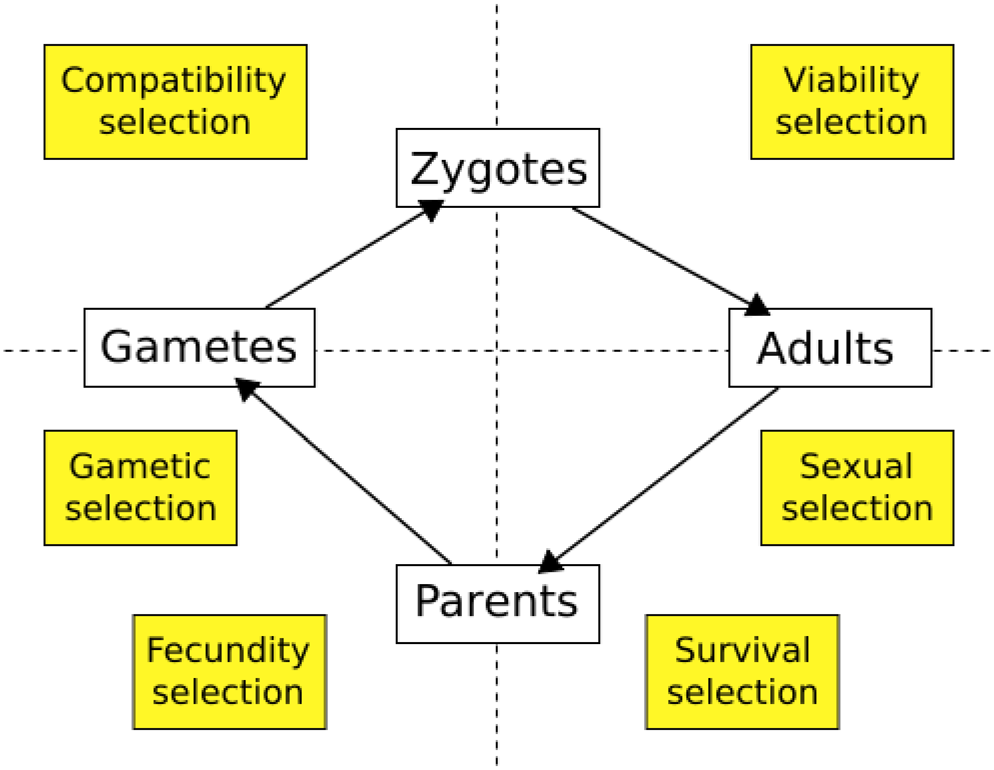
Though natural selection acts on individuals, the effects of chance mean that fitness can only really be defined "on average" for the individuals within a population. The fitness of a particular genotype corresponds to the average effect on all individuals with that genotype. Very low-fitness genotypes cause their bearers to have few or no offspring on average; examples include many human genetic disorders like cystic fibrosis.

Since fitness is an averaged quantity, it is also possible that a favorable mutation arises in an individual that does not survive to adulthood for unrelated reasons. Fitness also depends crucially upon the environment. Conditions like sickle-cell anemia may have low fitness in the general human population, but because the sickle-cell trait confers immunity from malaria, it has high fitness value in populations which have high malaria infection rates.

Types of selection

Natural selection can act on any heritable phenotypic trait, and selective pressure can be produced by any aspect of the environment, including sexual selection and competition with members of the same or other species. However, this does not imply that natural selection is always directional and results in adaptive evolution; natural selection often results in the maintenance of the status quo by eliminating less fit variants.

The unit of selection can be the individual or it can be another level within the hierarchy of biological organisation, such as genes, cells, and kin groups. There is still debate about whether natural selection acts at the level of groups or species to produce adaptations that benefit a larger, non-kin group. Selection at a different level such as the gene can result in an increase in fitness for that gene, while at the same time reducing the fitness of the individuals carrying that gene, in a process called intragenomic conflict. Overall, the combined effect of all selection pressures at various levels determines the overall fitness of an individual, and hence the outcome of natural selection.



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The life cycle of a sexually reproducing organism. Various components of natural selection are indicated for each life stage.

Natural selection occurs at every life stage of an individual. An individual organism must survive until adulthood before it can reproduce, and selection of those that reach this stage is called *viability selection*. In many species, adults must compete with each other for mates via sexual selection, and success in this competition determines who will parent the next generation. When individuals can reproduce more than once, a longer survival in the reproductive phase increases the number of offspring, called *survival selection*.

The fecundity of both females and males (for example, giant sperm in certain species of *Drosophila*) can be limited via "fecundity selection". The viability of produced gametes can differ, while intragenomic conflicts such as meiotic drive between the haploid gametes can result in gametic or "genic selection". Finally, the union of some combinations of eggs and sperm might be more compatible than others; this is termed *compatibility selection*.

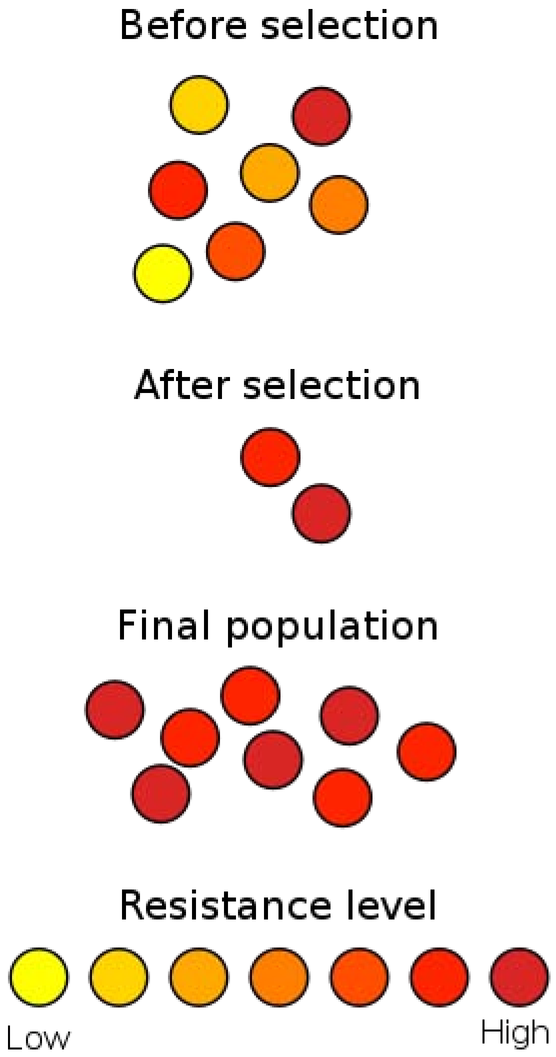
Sexual selection

It is useful to distinguish between "ecological selection" and "sexual selection". Ecological selection covers any mechanism of selection as a result of the environment (including relatives, e.g. kin selection, competition, and infanticide), while "sexual selection" refers specifically to competition for mates.

Sexual selection can be *intrasexual*, as in cases of competition among individuals of the same sex in a population, or *intersexual*, as in cases where one sex controls reproductive access by choosing among a population of available mates. Most commonly, intrasexual selection involves male–male competition and intersexual selection involves female choice of suitable males, due to the generally greater investment of resources for a female than a male in a single offspring. However, some species exhibit sex-role reversed behavior in which it is males that are most selective in mate choice; the best-known examples of this pattern occur in some fishes of the family *Syngnathidae*, though likely examples have also been found in amphibian and bird species.

Some features that are confined to one sex only of a particular species can be explained by selection exercised by the other sex in the choice of a mate, for example, the extravagant plumage of some male birds. Similarly, aggression between members of the same sex is sometimes associated with very distinctive features, such as the antlers of stags, which are used in combat with other stags. More generally, intrasexual selection is often associated with sexual dimorphism, including differences in body size between males and females of a species.

Examples of natural selection



Resistance to antibiotics is increased though the survival of individuals which are immune to the effects of the antibiotic, whose offspring then inherit the resistance, creating a new population of resistant bacteria.

A well-known example of natural selection in action is the development of antibiotic resistance in microorganisms. Since the discovery of penicillin in 1928 by Alexander Fleming, antibiotics have been used to fight bacterial diseases. Natural populations of bacteria contain, among their vast numbers of individual members, considerable variation in their genetic material, primarily as the result of mutations. When exposed to antibiotics, most bacteria die quickly, but some may have mutations that make them slightly less susceptible. If the exposure to antibiotics is short, these individuals will survive the treatment. This selective elimination of maladapted individuals from a population is natural selection.

These surviving bacteria will then reproduce again, producing the next generation. Due to the elimination of the maladapted individuals in the past generation, this population contains more bacteria that have some resistance against the antibiotic. At the same time, new mutations occur, contributing new genetic variation to the existing genetic variation. Spontaneous mutations are very rare, and advantageous mutations are even rarer. However, populations of bacteria are large enough that a few individuals will have beneficial mutations. If a new mutation reduces their susceptibility to an antibiotic, these individuals are more likely to survive when next confronted with that antibiotic.

Given enough time, and repeated exposure to the antibiotic, a population of antibiotic-resistant bacteria will emerge. This new changed population of antibiotic-resistant bacteria is optimally adapted to the context it evolved in. At the same time, it is not necessarily optimally adapted any more to the old antibiotic free environment. The end result of natural selection is two populations that are both optimally adapted to their specific environment, while both perform substandard in the other environment.

The widespread use and misuse of antibiotics has resulted in increased microbial resistance to antibiotics in clinical use, to the point that the methicillin-resistant *Staphylococcus aureus* (MRSA) has been described as a "superbug" because of the threat it poses to health and its relative invulnerability to existing drugs. Response strategies typically include the use of different, stronger antibiotics; however, new strains of MRSA have recently emerged that are resistant even to these drugs.

This is an example of what is known as an evolutionary arms race, in which bacteria continue to develop strains that are less susceptible to antibiotics, while medical researchers continue to develop new antibiotics that can kill them. A similar situation occurs with pesticide resistance in plants and insects. Arms races are not necessarily induced by man; a well-documented example involves the spread of a gene in the butterfly Hypolimnas bolina suppressing male-killing activity by Wolbachia bacteria parasites on the island of Samoa, where the spread of the gene is known to have occurred over a period of just five years

Evolution by means of natural selection

A prerequisite for natural selection to result in adaptive evolution, novel traits and speciation, is the presence of heritable genetic variation that results in fitness differences. Genetic variation is the result of mutations, recombinations and alterations in the karyotype (the number, shape, size and internal arrangement of the chromosomes). Any of these changes might have an effect that is highly advantageous or highly disadvantageous, but large effects are very rare. In the past, most changes in the genetic material were considered neutral or close to neutral because they occurred in noncoding DNA or resulted in a synonymous substitution. However, recent research suggests that many mutations in non-coding DNA do have slight deleterious effects. Although both mutation rates and average fitness effects of mutations are dependent on the organism, estimates from data in humans have found that a majority of mutations are slightly deleterious.

The exuberant tail of the peacock is thought to be the result of sexual selection by females. This peacock is an albino; selection against albinos in nature is intense because they are easily spotted by predators or are unsuccessful in competition for mates.

By the definition of fitness, individuals with greater fitness are more likely to contribute offspring to the next generation, while individuals with lesser fitness are more likely to die early or fail to reproduce. As a result, alleles which on average result in greater fitness become more abundant in the next generation, while alleles which generally reduce fitness become rarer. If the selection forces remain the same for many generations, beneficial alleles become more and more abundant, until they dominate the population, while alleles with a lesser fitness disappear. In every generation, new mutations and re-combinations arise spontaneously, producing a new spectrum of phenotypes. Therefore, each new generation will be enriched by the increasing abundance of alleles that contribute to those traits that were favored by selection, enhancing these traits over successive generations.

Some mutations occur in so-called regulatory genes. Changes in these can have large effects on the phenotype of the individual because they regulate the function of many other genes. Most, but not all, mutations in regulatory genes result in non-viable zygotes. Examples of nonlethal regulatory mutations occur in HOX genes in humans, which can result in a cervical rib or polydactyly, an increase in the number of fingers or toes. When such mutations result in a higher fitness, natural selection will favor these phenotypes and the novel trait will spread in the population.

X-ray of the left hand of a ten year old boy with polydactyly.

Established traits are not immutable; traits that have high fitness in one environmental context may be much less fit if environmental conditions change. In the absence of natural selection to preserve such a trait, it will become more variable and deteriorate over time, possibly resulting in a vestigial manifestation of the trait, also called evolutionary baggage. In many circumstances, the apparently vestigial structure may retain a limited functionality, or may be co-opted for other advantageous traits in a phenomenon known as preadaptation. A famous example of a vestigial structure, the eye of the blind mole rat, is believed to retain function in photoperiod perception.

Speciation

Speciation requires selective mating, which result in a reduced gene flow. Selective mating can be the result of 1. Geographic isolation, 2. Behavioral isolation, or 3. Temporal isolation. For example, a change in the physical environment (geographic isolation by an extrinsic barrier) would follow number 1, a change in camouflage for number 2 or a shift in mating times (i.e., one species of deer shifts location and therefore changes its "rut") for number 3.

Over time, these subgroups might diverge radically to become different species, either because of differences in selection pressures on the different subgroups, or because different mutations arise spontaneously in the different populations, or because of founder effects – some potentially beneficial alleles may, by chance, be present in only one or other of two subgroups when they first become separated. A lesser-known mechanism of speciation occurs via hybridization, well-documented in plants and occasionally observed in species-rich groups of animals such as cichlid fishes. Such mechanisms of rapid speciation can reflect a mechanism of evolutionary change known as punctuated equilibrium, which suggests that evolutionary change and particularly speciation typically happens quickly after interrupting long periods of stasis.

Genetic changes within groups result in increasing incompatibility between the genomes of the two subgroups, thus reducing gene flow between the groups. Gene flow will effectively cease when the distinctive mutations characterizing each subgroup become fixed. As few as two mutations can result in speciation: if each mutation has a neutral or positive effect on fitness when they occur separately, but a negative effect when they occur together, then fixation of these genes in the respective subgroups will lead to two reproductively isolated populations. According to the biological species concept, these will be two different species.

Historical development

The modern theory of natural selection derives from the work of Charles Darwin in the nineteenth century.

Pre-Darwinian theories

Several ancient philosophers expressed the idea that nature produces a huge variety of creatures, apparently randomly, and that only those creatures survive that manage to provide for themselves and reproduce successfully; well-known examples include Empedocles and his intellectual successor, Lucretius, while related ideas were later refined by Aristotle. The struggle for existence was later described by Al-Jahiz, who argued that environmental factors influence animals to develop new characteristics to ensure survival.

Abu Rayhan Biruni described the idea of artificial selection and argued that nature works in much the same way. Similar ideas were later expressed by Nasir al-Din Tusi and Ibn Khaldun. Such classical arguments were reintroduced in the 18th century by Pierre Louis Maupertuis and others, including Charles Darwin's grandfather Erasmus Darwin. While these forerunners had an influence on Darwinism, they later had little influence on the trajectory of evolutionary thought after Charles Darwin.

Until the early 19th century, the prevailing view in Western societies was that differences between individuals of a species were uninteresting departures from their Platonic idealism (or typus) of created kinds. However, the theory of uniformitarianism in geology promoted the idea that simple, weak forces could act continuously over long periods of time to produce radical changes in the Earth's landscape. The success of this theory raised awareness of the vast scale of geological time and made plausible the idea that tiny, virtually imperceptible changes in successive generations could produce consequences on the scale of differences between species.

Early 19th century evolutionists such as Jean Baptiste Lamarck suggested the inheritance of acquired characteristics as a mechanism for evolutionary change; adaptive traits acquired by an organism during its lifetime could be inherited by that organism's progeny, eventually causing transmutation of species. This theory has come to be known as Lamarckism and was an influence on the anti-genetic ideas of the Stalinist Soviet biologist Trofim Lysenko.

Darwin's theory

In 1859, Charles Darwin set out his theory of evolution by natural selection as an explanation for adaptation and speciation. He defined natural selection as the "principle by which each slight variation [of a trait], if useful, is preserved". The concept was simple but powerful: individuals best adapted to their environments are more likely to survive and reproduce. As long as there is some variation between them, there will be an inevitable selection of individuals with the most advantageous variations. If the variations are inherited, then differential reproductive success will lead to a progressive evolution of particular populations of a species, and populations that evolve to be sufficiently different eventually become different species.

Darwin's ideas were inspired by the observations that he had made on the *Beagle* voyage, and by the work of a political economist, the Reverend Thomas Malthus, who in *An Essay on the Principle of Population*, noted that population (if unchecked) increases exponentially whereas the food supply grows only arithmetically; thus inevitable limitations of resources would have demographic implications, leading to a "struggle for existence". When Darwin read Malthus in 1838 he was already primed by his work as a naturalist to appreciate the "struggle for existence" in nature and it struck him that as population outgrew resources, "favourable variations would tend to be preserved, and unfavourable ones to be destroyed. The result of this would be the formation of new species."

Here is Darwin's own summary of the idea, which can be found in the fourth chapter of the *Origin*:

> If during the long course of ages and under varying conditions of life, organic beings vary at all in the several parts of their organisation, and I think this cannot be disputed; if there be, owing to the high geometrical powers of increase of each species, at some age, season, or year, a severe struggle for life, and this certainly

> cannot be disputed; then, considering the infinite complexity of the relations of all organic beings to each other and to their conditions of existence, causing an infinite diversity in structure, constitution, and habits, to be advantageous to them, I think it would be a most extraordinary fact if no variation ever had occurred useful to each being's own welfare, in the same way as so many variations have occurred useful to man. But if variations useful to any organic being do occur, assuredly individuals thus characterised will have the best chance of being preserved in the struggle for life; and from the strong principle of inheritance they will tend to produce offspring similarly characterised. This principle of preservation, I have called, for the sake of brevity, Natural Selection.

Once he had his theory "by which to work", Darwin was meticulous about gathering and refining evidence as his "prime hobby" before making his idea public. He was in the process of writing his "big book" to present his researches when the naturalist Alfred Russel Wallace independently conceived of the principle and described it in an essay he sent to Darwin to forward to Charles Lyell. Lyell and Joseph Dalton Hooker decided (without Wallace's knowledge) to present his essay together with unpublished writings which Darwin had sent to fellow naturalists, and *On the Tendency of Species to form Varieties; and on the Perpetuation of Varieties and Species by Natural Means of Selection* was read to the Linnean Society announcing co-discovery of the principle in July 1858. Darwin published a detailed account of his evidence and conclusions in *On the Origin of Species* in 1859. In the 3rd edition of 1861 Darwin acknowledged that others — notably William Charles Wells in 1813, and Patrick Matthew in 1831 — had proposed similar ideas, but had neither developed them nor presented them in notable scientific publications.

Darwin thought of natural selection by analogy to how farmers select crops or livestock for breeding, which he called "artificial selection"; in his early manuscripts he referred to a 'Nature' which would do the selection. At the time, other mechanisms of evolution such as evolution by genetic drift were not yet explicitly formulated, and Darwin believed that selection was likely only part of the story: "I am convinced that [it] has been the main, but not exclusive means of modification." In a letter to Charles Lyell in September 1860, Darwin regretted the use of the term "Natural Selection", preferring the term "Natural Preservation".

For Darwin and his contemporaries, natural selection was essentially synonymous with evolution by natural selection. After the publication of *On the Origin of Species*, educated people generally accepted that evolution had occurred in some form. However, natural selection remained controversial as a mechanism, partly because it was perceived to be too weak to explain the range of observed characteristics of living organisms, and partly because even supporters of evolution balked at its "unguided" and non-progressive nature, a response that has been characterized as the single most significant impediment to the idea's acceptance.

However, some thinkers enthusiastically embraced natural selection; after reading Darwin, Herbert Spencer introduced the term *survival of the fittest*, which became a popular summary of the theory. The fifth edition of *On the Origin of Species* published in 1869 included Spencer's phrase as an alternative to natural selection, with credit given: "But the expression often used by Mr. Herbert Spencer, of the Survival of the Fittest, is more accurate, and is sometimes equally convenient." Although the phrase is still often used by non-biologists, modern biologists avoid it because it is tautological if "fittest" is read to mean "functionally superior" and is applied to individuals rather than considered as an averaged quantity over populations.

Modern evolutionary synthesis

Natural selection relies crucially on the idea of heredity, but it was developed long before the basic concepts of genetics. Although the Austrian monk Gregor Mendel, the father of modern genetics, was a contemporary of Darwin's, his work would lie in obscurity until the early 20th century. Only after the integration of Darwin's theory of evolution with a complex statistical appreciation of Gregor Mendel's 're-discovered' laws of inheritance did natural selection become generally accepted by scientists.

The work of Ronald Fisher (who developed the required mathematical language and The Genetical Theory of Natural Selection), J.B.S. Haldane (who introduced the concept of the "cost" of natural selection), Sewall Wright (who elucidated the nature of selection and adaptation), Theodosius Dobzhansky, William Hamilton (who conceived of kin selection), Ernst Mayr (who recognised the key importance of reproductive isolation for speciation) and many others formed the modern evolutionary synthesis. This synthesis cemented natural selection as the foundation of evolutionary theory, where it remains today.

Impact of the idea

Darwin's ideas, along with those of Adam Smith and Karl Marx, had a profound influence on 19th century thought. Perhaps the most radical claim of the theory of evolution through natural selection is that "elaborately constructed forms, so different from each other, and dependent on each other in so complex a manner" evolved from the simplest forms of life by a few simple principles. This claim inspired some of Darwin's most ardent supporters—and provoked the most profound opposition. The radicalism of natural selection, according to Stephen Jay Gould, lay in its power to "dethrone some of the deepest and most traditional comforts of Western thought". In particular, it challenged long-standing beliefs in such concepts as a special and exalted place for humans in the natural world and a benevolent creator whose intentions were reflected in nature's order and design.

Cell and molecular biology

In the 19th century, Wilhelm Roux, a founder of modern embryology, wrote a book entitled « Der Kampf der Teile im Organismus » (The struggle of parts in the organism) in which he suggested that the development of an organism results from a Darwinian competition between the parts of the embryo, occurring at all levels, from molecules to organs. In recent years, a modern version of this theory has been proposed by Jean-Jacques Kupiec. According to this cellular Darwinism, stochasticity at the molecular level generates diversity in cell types whereas cell interactions impose a characteristic order on the developing embryo.

Social and psychological theory

The social implications of the theory of evolution by natural selection also became the source of continuing controversy. Friedrich Engels, a German political philosopher and co-originator of the ideology of communism, wrote in 1872 that "Darwin did not know what a bitter satire he wrote on mankind when he showed that free competition, the struggle for existence, which the economists celebrate as the highest historical achievement, is the normal state of the animal kingdom". Interpretation of natural selection as necessarily 'progressive', leading to increasing 'advances' in intelligence and civilisation, was used as a justification for colonialism and policies of eugenics, as well as broader sociopolitical positions now described as Social Darwinism. Konrad Lorenz won the Nobel Prize in Physiology or Medicine in 1973 for his analysis of animal behavior in terms of the role of natural selection (particularly group selection). However, in Germany in 1940, in writings that he subsequently disowned, he used the theory as a justification for policies of the Nazi state. He wrote "... selection for toughness, heroism, and social utility...must be accomplished by some human institution, if mankind, in default of selective factors, is not to be ruined by domestication-induced degeneracy. The racial idea as the basis of our state has already accomplished much in this respect." Others have developed ideas that human societies and culture evolve by mechanisms that are analogous to those that apply to evolution of species.

More recently, work among anthropologists and psychologists has led to the development of sociobiology and later evolutionary psychology, a field that attempts to explain features of human psychology in terms of adaptation to the ancestral environment. The most prominent such example, notably advanced in the early work of Noam Chomsky and later by Steven Pinker, is the hypothesis that the human brain is adapted to acquire the grammatical rules of natural language. Other aspects of human behavior and social structures, from specific cultural norms such as incest avoidance to broader patterns such as gender roles, have been hypothesized to have similar origins as adaptations to the early environment in which modern humans evolved. By analogy to the action of natural selection on genes, the concept of memes – "units of cultural transmission", or culture's equivalents of genes undergoing selection and recombination – has arisen, first described in this form by Richard Dawkins and subsequently expanded upon by philosophers such as Daniel Dennett as explanations for complex cultural activities, including human consciousness. Extensions of the theory of natural selection to such a wide range of cultural phenomena have been distinctly controversial and are not widely accepted.

Information and systems theory

In 1922, Alfred Lotka proposed that natural selection might be understood as a physical principle which could be described in terms of the use of energy by a system, a concept that was later developed by Howard Odum as the maximum power principle whereby evolutionary systems with selective advantage maximise the rate of useful energy transformation. Such concepts are sometimes relevant in the study of applied thermodynamics.

The principles of natural selection have inspired a variety of computational techniques, such as "soft" artificial life, that simulate selective processes and can be highly efficient in 'adapting' entities to an environment defined by a specified fitness function. For example, a class of heuristic optimization algorithms known as genetic algorithms, pioneered by John Holland in the 1970s and expanded upon by David E. Goldberg, identify optimal solutions by simulated reproduction and mutation of a population of solutions defined by an initial probability distribution. Such algorithms are particularly useful when applied to problems whose solution landscape is very rough or has many local minima.

Genetic basis of natural selection

The idea of natural selection predates the understanding of genetics. We now have a much better idea of the biology underlying heritability, which is the basis of natural selection.

Genotype and phenotype

Natural selection acts on an organism's phenotype, or physical characteristics. Phenotype is determined by an organism's genetic make-up (genotype) and the environment in which the organism lives. Often, natural selection acts on specific traits of an individual, and the terms phenotype and genotype are used narrowly to indicate these specific traits.

When different organisms in a population possess different versions of a gene for a certain trait, each of these versions is known as an allele. It is this genetic variation that underlies phenotypic traits. A typical example is that certain combinations of genes for eye color in humans which, for instance, give rise to the phenotype of blue eyes. (On the other hand, when all the organisms in a population share the same allele for a particular trait, and this state is stable over time, the allele is said to be *fixed* in that population.)

Some traits are governed by only a single gene, but most traits are influenced by the interactions of many genes. A variation in one of the many genes that contributes to a trait may have only a small effect on the phenotype; together, these genes can produce a continuum of possible phenotypic values.

Directionality of selection

When some component of a trait is heritable, selection will alter the frequencies of the different alleles, or variants of the gene that produces the variants of the trait. Selection can be divided into three classes, on the basis of its effect on allele frequencies.

Directional selection occurs when a certain allele has a greater fitness than others, resulting in an increase of its frequency. This process can continue until the allele is fixed and the entire population shares the fitter phenotype. It is directional selection that is illustrated in the antibiotic resistance example above.

Far more common is stabilizing selection (which is commonly **confused** with *purifying selection*), which lowers the frequency of alleles that have a deleterious effect on the phenotype – that is, produce organisms of lower fitness. This process can continue until the allele is eliminated from the population. Purifying selection results in functional genetic features, such as protein-coding genes or regulatory sequences, being conserved over time due to selective pressure against deleterious variants.

Finally, a number of forms of balancing selection exist, which do not result in fixation, but maintain an allele at intermediate frequencies in a population. This can occur in diploid species (that is, those that have two pairs of chromosomes) when heterozygote individuals, who have different alleles on each chromosome at a single genetic locus, have a higher fitness than homozygote individuals that have two of the same alleles. This is called heterozygote advantage or overdominance, of which the best-known example is the malarial resistance observed in heterozygous humans who carry only one copy of the gene for sickle cell anemia. Maintenance of allelic variation can also occur through disruptive or diversifying selection, which favors genotypes that depart from the average in either direction (that is, the opposite of overdominance), and can result in a bimodal distribution of trait values. Finally, balancing selection can occur through frequency-dependent selection, where the fitness of one particular phenotype depends on the distribution of other phenotypes in the population. The principles of game theory have been applied to understand the fitness distributions in these situations, particularly in the study of kin selection and the evolution of reciprocal altruism.

Selection and genetic variation

A portion of all genetic variation is functionally neutral in that it produces no phenotypic effect or significant difference in fitness; the hypothesis that this variation accounts for a large fraction of observed genetic diversity is known as the neutral theory of molecular evolution and was originated by Motoo Kimura. When genetic variation does not result in differences in fitness, selection cannot *directly* affect the frequency of such variation. As a result, the genetic variation at those sites will be higher than at sites where variation does influence fitness. However, after a period with no new mutation, the genetic variation at these sites will be eliminated due to genetic drift.

Mutation selection balance

Natural selection results in the reduction of genetic variation through the elimination of maladapted individuals and consequently of the mutations that caused the maladaptation. At the same time, new mutations occur, resulting in a mutation-selection balance. The exact outcome of the two processes depends both on the rate at which new mutations occur and on the strength of the natural selection, which is a function of how unfavorable the mutation proves to be. Consequently, changes in the mutation rate or the selection pressure will result in a different mutation-selection balance.

Genetic linkage

Genetic linkage occurs when the loci of two alleles are *linked*, or in close proximity to each other on the chromosome. During the formation of gametes, recombination of the genetic material results in reshuffling of the alleles. However, the chance that such a reshuffle occurs between two alleles depends on the distance between those alleles; the closer the alleles are to each other, the less likely it is that such a reshuffle will occur. Consequently, when selection targets one allele, this automatically results in selection of the other allele as well; through this mechanism, selection can have a strong influence on patterns of variation in the genome.

Selective sweeps occur when an allele becomes more common in a population as a result of positive selection. As the prevalence of one allele increases, linked alleles can also become more common, whether they are neutral or even slightly deleterious. This is called *genetic hitchhiking*. A strong selective sweep results in a region of the genome where the positively selected haplotype (the allele and its neighbours) are essentially the only ones that exist in the population.

Whether a selective sweep has occurred or not can be investigated by measuring linkage disequilibrium, or whether a given haplotype is overrepresented in the population. Normally, genetic recombination results in a reshuffling of the different alleles within a haplotype, and none of the haplotypes will dominate the population. However, during a selective sweep, selection for a specific allele will also result in selection of neighbouring alleles. Therefore, the presence of a block of strong linkage disequilibrium might indicate that there has been a 'recent' selective sweep near the center of the block, and this can be used to identify sites recently under selection.

Background selection is the opposite of a selective sweep. If a specific site experiences strong and persistent purifying selection, linked variation will tend to be weeded out along with it, producing a region in the genome of low overall variability. Because background selection is a result of deleterious new mutations, which can occur randomly in any haplotype, it does not produce clear blocks of linkage disequilibrium, although with low recombination it can still lead to slightly negative linkage disequilibrium overall.

Green-beard effect

The gene-centered view of evolution postulates that natural selection will increase the frequency of those genes whose phenotypic effects ensure their successful replication. A gene for altruism can be favored by selection if the altruism is primarily directed at other individuals who share the same gene (kin selection).

A **green-beard effect** occurs when a gene, or linked genes, produce three phenotypic effects:

1. a perceptible trait — the hypothetical "green beard";
2. recognition of this trait in others; and
3. preferential treatment to those recognized.

So this gene is directly recognizing copies of itself, regardless of average relatedness. Whereas most alleles that are favored by kin selection spread by promoting altruism towards those likely to be carrying the same allele, green-beard alleles would rise to frequency by promoting altruism toward individuals certain to be carrying the same allele.

Green-beard altruism could increase the presence of green-beard phenotypes in a population even if genes are assisting other genes that are not exact copies of themselves in a molecular sense; all that is required is that they produce the three phenotypic characteristics described above. Green beard genes are vulnerable to mutant genes arising that produce the perceptible trait without the helping behaviour.

The idea of a green-beard gene was proposed by William D. Hamilton in his articles of 1964, and named as "Green Beard" by Richard Dawkins in *The Selfish Gene* (1976).

Examples

In the last several years, evolutionary biologists have questioned the potential validity of greenbeard alleles, suggesting it would be extraordinarily rare for a single allele to produce three complex phenotypic effects. This criticism has led some to believe that they simply cannot exist or that they only can be present in less complex organisms, such as microorganisms. Several discoveries within the past ten years have illuminated the validity of this critique.

The concept remained a merely theoretical possibility under Dawkins' selfish gene model until 1998, when a green-beard gene was first found in nature, in the red imported fire ant (*Solenopsis invicta*). Polygyne colony queens are heterozygous (Bb) at the Gp-9 gene locus. The investigators discovered that homozygous dominant (BB) queens are specifically killed, most often by heterozygous workers (Bb) and not homozygous dominants (BB). They concluded that the allele Gp-9^b is linked to a greenbeard allele which induces workers bearing this allele to kill all queens that do not have it. A final conclusion notes that the workers are able to distinguish BB queens from Bb queens based on an odor cue.

The gene csA in *Dictyostelium discoideum*, discovered in 2003, codes for a cell adhesion protein which binds to gp80 proteins on other cells, allowing multicellular fruiting body formation on soil. Mixtures of csA knockout cells with wild-type cells yield spores, “born” from the fruiting bodies, which are 82% wild-type (WT). This is because the wild-type cells are better at adhering and more effectively combine into aggregates; knockout

(KO) cells are left behind. On more adhesive but less natural substances, KO cells can adhere; WT cells, still better at adhering, sort preferentially into the stalk.

In 2006, green beard-like recognition was seen in the cooperative behavior among color morphs in side-blotched lizards, although the traits appear to be encoded by multiple loci across the genome.

A more recent example, found in 2008, is a gene that makes brewer's yeast clump together in response to a toxin such as alcohol. By investigating flocculation, a type of self-adherence generally present in asexual aggregations, Smukalla *et al.* showed that *S. cerevisiae* is a model for cooperative behavior evolution. When this yeast expresses FLO1 in the laboratory, flocculation is restored. Flocculation is apparently protective for the FLO1+ cells, which are shielded from certain stresses (ethanol, for example). In addition FLO1+ cells preferentially adhere to each other. The authors therefore conclude that flocculation is driven by this greenbeard gene.

Intragenomic conflict

The selfish gene theory postulates that natural selection will increase the frequency of those genes whose phenotypic effects ensure their successful replication. Generally, a gene achieves this goal by building, in cooperation with other genes, an organism capable of transmitting the gene to descendants. **Intragenomic conflict** arises when genes inside a genome are not transmitted by the same rules, or when a gene causes its own transmission to the detriment of the rest of the genome (this last kind of gene is usually called selfish genetic element, or ultraselfish gene or parasitic DNA).

Nuclear genes

This section deals with conflict between nuclear genes.

Meiotic drive

All nuclear genes in a given diploid genome cooperate because each allele has an equal probability of being present in a gamete. This fairness is guaranteed by meiosis. However, there is one type of gene, called a segregation distorter, that "cheats" during meiosis or gametogenesis and thus is present in more than half of the functional gametes. The most studied examples are sd in *Drosophila melanogaster* (fruit fly), t haplotype in *Mus musculus* (mouse) and sk in *Neurospora sp.* (fungus). Segregation distorters that are present in sexual chromosomes (as the X chromosome in several *Drosophila* species) are denominated sex-ratio distorters, as they induce a sex-ratio bias in the offspring of the carrier individual.

Killer and target

The most simple model of meiotic drive involves two tightly linked loci: a *Killer* locus and a *Target* locus. The segregation distorter set is composed by the allele *Killer* (in the *Killer* locus) and the allele *Resistant* (in the *Target* locus), while its rival set is composed by the alleles *Non-killer* and *Non-resistant*. So, the segregation distorter set produces a toxin to which it is itself resistant, while its rival is not. Thus, it kills those gametes containing the rival set and increases in frequency. The tight linkage between these loci is crucial, so these genes usually lie on low recombination regions of the genome.

True meiotic drive

Other systems do not involve gamete destruction, but rather use the asymmetry of meiosis in females: the driving allele ends up in the ovocyte instead of in the polar bodies with a probability greater than one half. This is termed true meiotic drive, as it does not rely on a post-meiotic mechanism. The best-studied examples include the neocentromeres (knobs) of maize, as well as several chromosomal rearrangements in mammals. The general molecular evolution of centromeres is likely to involve such mechanisms.

Lethal Maternal-effects

The Medea gene causes the death of progeny from a heterozygous mother that do not inherit it. It occurs in the flour beetle (*Tribolium castaneum*). Maternal-effect selfish genes have been successfully synthesized in the lab.

Transposons

Transposons are autonomous replicating genes that encode the ability to move to new positions in the genome and therefore accumulate in the genomes. They replicate themselves in spite of being detrimental to the rest of the genome. They are often called 'jumping genes' or parasitic DNA and were discovered by Barbara McClintock in 1944.

Homing endonuclease genes

Homing endonuclease genes (HEG) convert their rival allele into a copy of themselves, and are thus inherited by nearly all meiotic daughter cells of a heterozygote cell. They achieve this by encoding an endonuclease which breaks the rival allele. This break is repaired by using the sequence of the HEG as template.

HEGs encode sequence-specific endonucleases. The recognition sequence (RS) is 15-30 bp long and usually occurs once in the genome. HEGs are located in the middle of their own recognition sequences. Most HEGs are encoded by self-splicing introns (group I & II) and inteins. Inteins are internal protein fragments produced from protein splicing and usually contain endonuclease and splicing activities. The allele without the HEGs are cleaved by the homing endonuclease and the double-strand break are repaired by homologous recombination (gene conversion) using the allele containing HEGs as template. Both chromosomes will contain the HEGs after repair.

B-chromosome

B-chromosomes are nonessential chromosomes; not homologous with any member of the normal (A) chromosome set; morphologically and structurally different from the A's; and they are transmitted at higher-than-expected frequencies, leading to their accumulation in progeny. In some cases, there is strong evidence to support the contention that they are simply *selfish* and that they exist as *parasitic* chromosomes. They are found in all major taxonomic groupings of both plants and animals.

Cytoplasmic genes

This section deals with conflict between nuclear and cytoplasmic genes. Mitochondria represent one such example of a set of cytoplasmic genes, as do plasmids and bacteria which have integrated themselves into another species' cytoplasm.

Males as dead-ends to cytoplasmic genes

Anisogamy generally produces zygotes that inherit cytoplasmic elements exclusively from the female gamete. Thus, males represent dead-ends to these genes. Because of this fact, cytoplasmic genes have evolved a number of mechanisms to increase the production of female descendants and/or eliminate offspring not containing them.

Feminization

Male organisms are converted into females by cytoplasmic inherited protists (Microsporidia) or bacteria (*Wolbachia*), regardless of nuclear sex-determining factors. This occurs in amphipod and isopod Crustacea and Lepidoptera.

Male-killing

Male embryos (in the case of cytoplasmic inherited bacteria) or male larvae (in the case of Microsporidia) are killed. In the case of embryo death, this diverts investment from males to females who can transmit these cytoplasmic elements (for instance, in ladybird beetles, infected female hosts eat their dead male brothers, which is positive from the viewpoint of the bacterium). In the case of microsporidia-induced larval death, the agent is transmitted out of the male lineage (through which it cannot be transmitted) into the environment, where it may be taken up again infectiously by other individuals. Male-killing occurs in many insects. In the case of male embryo death, a variety of bacteria have been implicated, including *Wolbachia*.

Male-sterility

Anther tissue (male gametophyte) is killed by mitochondria in monoicous angiosperms, increasing energy and material spent in developing female gametophytes.

Parthenogenesis induction

In certain haplodiploid Hymenoptera and mites, in which males are produced asexually, *Wolbachia* and *Cardinium* can induce duplication of the chromosomes and thus convert the organisms into females. The cytoplasmic bacterium forces haploid cells to go through mitosis to produce diploid cells which therefore will be female. This produces an entirely female population. Interestingly, if antibiotics are administered to populations which have become asexual in this way, they revert back to sexuality instantly, as the cytoplasmic bacteria forcing this behaviour upon them is removed.

Cytoplasmic incompatibility

In many arthropods, zygotes produced by sperm of infected males and ova of non-infected females can be killed by *Wolbachia* or *Cardinium*.

Plasmids

Plasmids are additional circular chromosomes present in many bacteria. Most plasmids promote conjugation between their host and other bacteria, infecting new cytoplasms while retaining a copy inside the original host. Chromosomal genes are usually not transmitted. Therefore, they bear the costs of replicating the donated plasmid and the costs of increased exposure to viruses, but gain little in return (but the genes on plasmids may direct production of proteins that are beneficial to bacteria such as those that confer antibiotic resistance properties).

Koinophilia

Koinophilia is a term used by biologist Johan Koeslag, meaning that when sexual creatures seek a mate, they prefer that mate not to have any unusual, peculiar or deviant features.

Natural selection results, over the course of generations, in beneficial (or "fit") features replacing their disadvantageous counterparts. Thus, natural selection causes beneficial features to become increasingly more common with each generation, while the disadvantageous features become increasingly rare. A sexual creature, therefore, wishing to mate with a fit partner, would be expected to avoid individuals sporting unusual features, while being especially attracted to those individuals displaying a predominance of common or average features. This is termed "koinophilia". It has, as an important side effect, that mates displaying mutant features (the result of a genetic mutation) are also avoided. This, in itself, is also advantageous, because the vast majority of mutations are disadvantageous. Because it is impossible to judge whether a new mutation is beneficial or not, koinophilic creatures will avoid them all with equal determination, even if this means avoiding the very occasional beneficial mutation. Thus, koinophilia, although not perfect or infallible in its ability to distinguish fit from unfit mates, remains, on average, a very good strategy when choosing a mate. It will be right far more often than it will be wrong. Even when it is wrong, a koinophilic choice always ensures that the offspring will inherit a suite of thoroughly tried and tested features.

According to Koeslag, koinophilia provides very simple and obvious explanations for such evolutionary puzzles as the process of speciation, evolutionary stasis and punctuated equilibria, sex and the affordability of males, and the evolution of cooperation.

Introduction

This mating strategy, was first referred to as *koinophilia* by Johan H. Koeslag, from the Greek, *koinos*, meaning "the usual" or "common", and *philos*, meaning "fondness" or "love". It was independently identified in humans by Judith Langlois, who found that the average of two human faces was more attractive than either of the faces from which that average was derived. The more faces (of the same gender and age) that were used in the averaging process the more attractive and appealing the average face became.

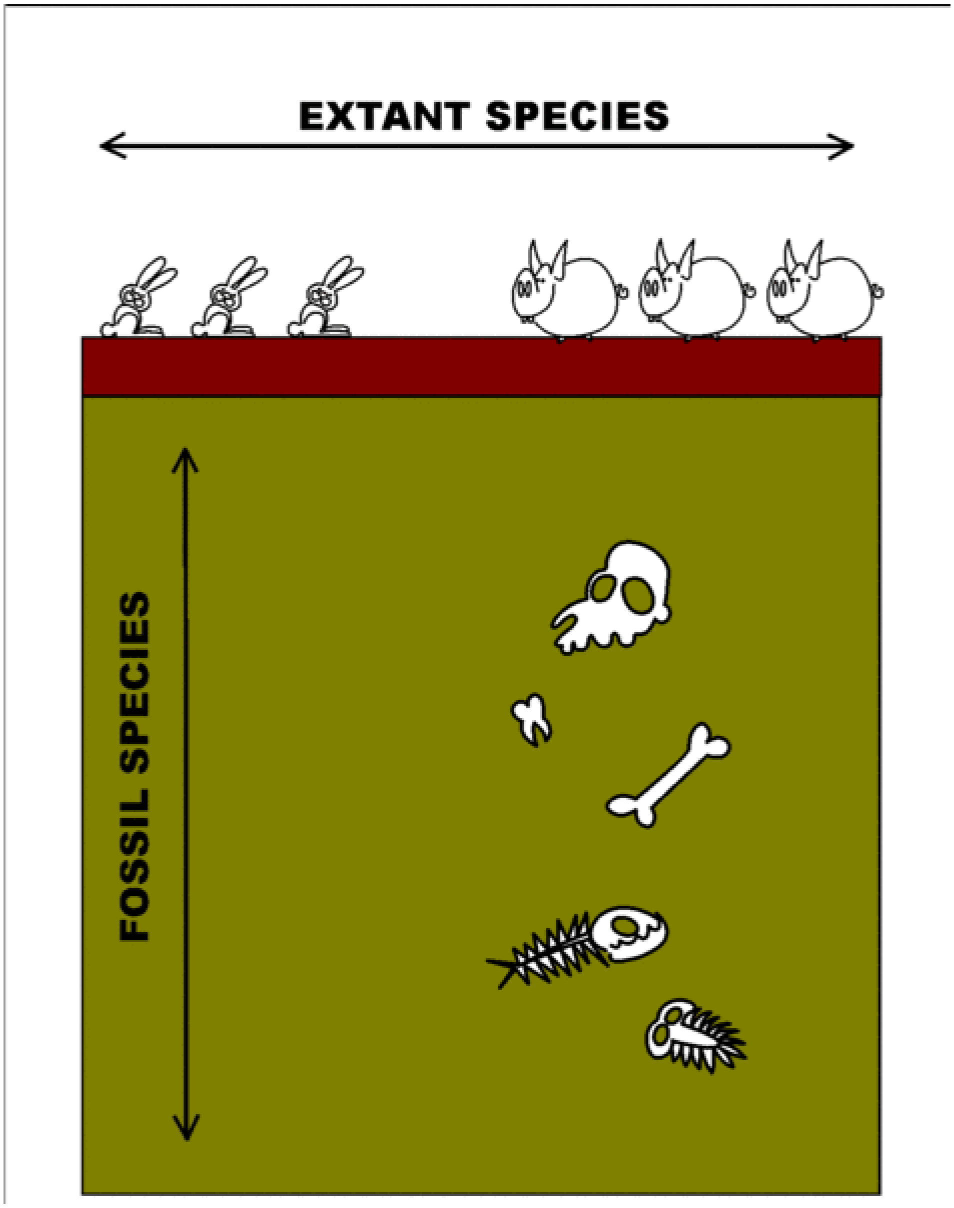
Physical attractiveness

In keeping with these theoretical considerations, one study on an isolated human population, as opposed to Western subjects, has suggested that preferences for averageness appear to be universal. The isolated people preferred average faces from their own race, but did not show any preference for average faces of other races. This makes sense since they are not exposed to outside races and thus have no knowledge of what an average face from another race looks like. This suggests that it is averageness alone, that is making a face attractive rather than some other artifact that results from averaging techniques . Many studies have confirmed that subjects find young average faces the most attractive. However, Perrett *et al.* found that both men and women considered that a face averaged from a set of attractive faces was more attractive than one averaged from a wide range of women's faces. When the differences between the first face and the second face were slightly exaggerated the new face was judged, on average, to be more attractive still. Although the three faces look remarkably similar, close examination of the photos in Perrett, May and Yoshikawa's paper shows, in fact, that the exaggerated face looks younger than the average face (composed of women's faces aged 22–46 years). Since the same results were obtained with Japanese subjects, these findings are probably culture independent, and would indicate that people generally find *youthful* average female faces sexually the most attractive, as expected.

Speciation and "punctuated equilibria"

The striking uniformity of the outward appearances of all the adult members of a species is a great evolutionary mystery.

A major evolutionary problem has been how the continuous process of evolution produces groups of individuals, labeled species, whose adult members look extraordinarily similar, and distinctively different from the members of other species. Lions and leopards are, for instance, both large carnivores inhabiting the same general environment, and hunting much the same prey, in much the same way, but they look extraordinarily different, and would not be confused one for the other even by the most unsophisticated observer. There would seem to be no obvious evolutionary reason which suggests that lion-leopard intermediates are likely to be less successful hunters than either of the two distinct species that inhabit the African savanna today. Why then do they not exist? What evolutionary force drives these intermediate forms to extinction, leaving only highly uniform and distinctive lions on the one hand and highly uniform and distinctive leopards on the other?



Speciation poses a "2-dimensional" problem. The discontinuities in appearance between existing species represent the "horizontal dimension" of the problem. The succession of fossil species represent the "vertical dimension".

This is, however, only one aspect of what is almost certainly a two-dimensional problem. The "horizontal" dimension refers to the almost complete absence of transitional, or intermediate forms between present-day species (e.g. between lions, leopards, cheetahs and lynxes). The "vertical" dimension concerns the fossil record. Fossil species are frequently remarkably stable over extremely long periods of geological time, despite continental drift, major climate changes, and mass extinctions. When a change in appearance or form does occur, it tends to be abrupt in geological terms, again producing phenotypic gaps (i.e. an absence of intermediate forms), but now between successive species, which then often co-exist for considerable periods of time. Thus the fossil record, though open to different interpretations, suggests that evolution occurs in bursts, interspersed by long periods of evolutionary stagnation (i.e. by means of punctuated equilibria). Why this is so, has been one of evolution's great mysteries.

Koinophilia could explain both the horizontal and vertical manifestations of speciation, and why it usually involves the entire external appearance of the creatures concerned. If sexual creatures prefer mates sporting predominantly common features, and avoid mates with unusual, unfamiliar, fringe, or extreme attributes, then common features will tend to become more common still, and at a rate and to an extent that natural selection on its own is unlikely to achieve. Since koinophilia affects the entire external appearance, the members of an interbreeding group will soon all begin to look astoundingly alike, both with regard to important or essential features (e.g. the jaws, dentition, and claws of a lion) and trivial features (e.g. the black furry tuft at the tip of the lion’s tail, or the lion's “beard”) . It is almost inevitable that each interbreeding group will, in this way, very quickly develop its own characteristic appearance. An individual from one group who wanders into another group will consequently be recognized as being different, and will, therefore, be discriminated against during the mating season. This koinophilia-induced reproductive isolation might thus be the first crucial step in the development of, ultimately, physiological, anatomical and behavioral barriers to hybridization, and thus, ultimately, full specieshood. Koinophilia will thereafter defend that species' appearance and behavior against invasion by unusual or unfamiliar forms (which might arise by immigration or mutation), and thus be a paradigm of punctuated equilibria (or the "vertical" aspect of the speciation problem.), and stabilizing selection.

The evolution of cooperation

Cooperative hunting by wolves allows them to tackle much larger and more nutritious prey than any individual wolf could handle. However, such cooperation could, potentially, be exploited by selfish individuals who do not expose themselves to the dangers of the hunt, but nevertheless share in the spoils.

Cooperation is any group behavior that benefits the individuals more than if they were to act as independent agents. There is, however, a second, very important, corollary to cooperation: it can always be exploited by selfish individuals who benefit even more by not taking part in the group activity, yet reaping its benefits. For instance, a selfish individual who does not join the hunting pack and its incumbent dangers but nevertheless shares in the spoils has a fitness advantage over the other members of the pack. Thus, although a group of cooperative individuals is fitter than an equivalent group of selfish individuals, selfish individuals interspersed amongst a community of cooperators are always fitter than their hosts. This means they raise, on average, more offspring and grandoffspring than their hosts, and will therefore ultimately replace them.

If, however, the selfish individuals are ostracized, and rejected as mates, because of their deviant and unusual behavior, then their evolutionary advantage becomes an evolutionary liability. Cooperation in all of its very many forms then becomes evolutionarily stable. Sociability, social conventions, ritualistic behavior, the expressions of the emotions, and other forms of communication between individuals, all essential ingredients for full cooperativity, can all be similarly evolutionarily stabilized by koinophilia.

Chapter- 5

Peppered Moth Evolution

Biston betularia f. typica, the white-bodied peppered moth.

Biston betularia f. carbonaria, the black-bodied peppered moth.

The **evolution of the peppered moth** over the last two hundred years has been studied in detail. Originally, the vast majority of peppered moths had light colouration, which effectively camouflaged them against the light-coloured trees and lichens which they rested upon. However, because of widespread pollution during the Industrial Revolution in England, many of the lichens died out, and the trees that peppered moths rested on became blackened by soot, causing most of the light-coloured moths, or ***typica***, to die off from predation. At the same time, the dark-coloured, or *melanic*, moths, ***carbonaria***, flourished because of their ability to hide on the darkened trees.

Since then, with improved environmental standards, light-coloured peppered moths have again become common, but the dramatic change in the peppered moth's population has remained a subject of much interest and study, and has led to the coining of the term ***industrial melanism*** to refer to the genetic darkening of species in response to pollutants. As a result of this relatively simple and easy-to-understand circumstances of the adaptation, the peppered moth has become a common example used in explaining or demonstrating natural selection.

Genetics

Evolution is defined as "a change in the frequency of an allele within a gene pool", an occurrence that causes a population's genetically inherited traits to change over successive generations. Evolution in the wild is chiefly caused by two mechanisms:

natural selection, the process by which individual organisms with beneficial traits are more likely to survive and reproduce, and genetic drift, the statistical drift over time of allele frequencies in a population from random sampling effects in the formation of successive generations.

J.W. Tutt first proposed the "differential bird predation hypothesis" in 1896, as a mechanism of natural selection. The melanic morphs were better camouflaged against the bark of trees without foliose lichen, whereas the *typica* morphs were better camouflaged against trees with lichens. As a result, birds would find and eat those morphs that were not camouflaged with increased frequency.

In 1924, J.B.S. Haldane calculated, using a simple general selection model, the selective advantage necessary for the recorded evolution of peppered moths, based on the assumption that in 1848 the frequency of dark-coloured moths was 2%, and by 1895 it was 95%. The dark-coloured, or melanic, form would have had to be one and a half times as fit as the typical, light-coloured form. Even taking into consideration the errors in the model, this reasonably excluded the stochastic process of genetic drift, because the changes were too fast.

In peppered moths, the allele for dark-bodied moths is dominant, while the allele for light-bodied moths is recessive, meaning that the *typica* moths have a phenotype (visible or detectable characteristic) that is only seen in a homozygous genotype (an organism that has two copies of the same allele), and never in a heterozygous one. This helps explain how dramatically quickly the population changed when being selected for dark colouration.

The peppered moth *Biston betularia* is also a model of parallel evolution in the incidence of melanism in the British form (f. carbonaria) and the American form (f. swettaria) as they are indistinguishable in appearance. Genetic analysis indicates that both phenotypes are inherited as autosomal dominants. Cross hybridizations indicate the phenotypes are produced by isoalleles at a single locus.

Environmental changes

Typica and *carbonaria* morphs resting on the same tree. The light-colored *typica* (below the bark's scar) is nearly invisible on this pollution-free tree, camouflaging it from predators.

Before the Industrial Revolution, the peppered moth was mostly found in a light grey form with little black speckled spots. The light-bodied moths were able to blend in with the light-coloured lichens and tree bark, and the less common black moth was more likely to be eaten by birds. As a result of the common light-coloured lichens and English trees, therefore, the light-coloured moths were much more effective at hiding from predators, and the frequency of the dark allele was about 0.01%.

During the early decades of the Industrial Revolution in England, the countryside between London and Manchester was blanketed with soot from the new coal-burning factories. Many of the light-bodied lichens died from sulphur dioxide emissions, and the trees became covered with soot. This led to an increase in bird predation for light-coloured moths, as they no longer blended in as well in their polluted ecosystem: indeed, their bodies now dramatically contrasted with the colour of the bark. Dark-coloured moths, on the other hand, were camouflaged very well by the blackened trees.

Although a majority of light-coloured moths initially continued to be produced, most of them didn't survive, while the dark-coloured moths flourished. As a result, over the course of many generations of moths, the allele frequency gradually shifted towards the dominant allele, as more and more dark-bodied moths survived to reproduce. By the mid-19th century, the number of dark-coloured moths had risen noticeably, and by 1895, the percentage of dark-coloured moths in the Manchester peppered moth population was reported at 98%, a dramatic change (by almost 1000%) from the original frequency. This evolved darkening in colour as a result of industrialization has come to be known as *industrial melanism* as a result.

While evidence of increasing frequency of melanic forms in the Lepidoptera was available during Darwin's lifetime — the first observations were made in 1848 — current understanding is that it was not until 1896, 14 years after Darwin's death, that Tutt explicitly linked melanism with natural selection. However, a recent article reports that melanism in the Lepidoptera had been linked to natural selection prior to Tutt. Albert Brydges Farn (1841–1921), a British entomologist, wrote to Darwin on the 18th November 1878 to discuss his observation of colour variations in the Annulet moth (then *Gnophos obscurata*, now *Charissa obscurata*). In his letter, Farn mentions the existence of different colour morphs, describing how each is matched to the habitats in which they are found (dark morphs on peat, white morphs on chalk cliffs) and refers explicitly to this variability as pointing to 'survival of the fittest'.

In modern times, because of cleaner air standards in Europe and North America, the dark-bodied moth is becoming less frequent, again demonstrating the adaptive shifts in the peppered moth population.

Rise and fall of phenotype frequency

Melanism has appeared in the European and North American peppered moth populations. Information about the rise in frequency is scarce. Much more is known about the subsequent fall in phenotype frequency, as it has been measured by lepidopterists using moth traps.

Though a black peppered moth was found in 1811, this can be seen as an aberrant morph caused by a recurrent mutation that was probably selected out of the population. The first *carbonaria* to be found was caught in Manchester, England in 1848, but was only reported 16 years later in 1864 by Edleston. Edleston notes that by 1864 it was the more common morph in his garden in Manchester. Steward compiled data for the first recordings of the peppered moth by locality, and deduced that the carbonaria morph was the result of a single mutation that subsequently spread. By 1895, it had reached a reported frequency of 98% in Manchester.

From around 1962 to the present, the phenotype frequency of *carbonaria* has steadily fallen. Its decline has been measured more accurately than its rise, because of more rigorous scientific studies being conducted. Notably, Bernard Kettlewell conducted a national survey in 1956, Bruce Grant conducted a similar one in early 1996. , and L.M. Cook in 2003.

Similar results were found in America. Melanic forms have not been found in Japan. It is believed that this is because peppered moths in Japan do not inhabit industrialised regions.

Predation experiments

The Great Tit, an insectivorous bird.

In 1896 J. W. Tutt hypothesised that the increased proportion of *carbonaria* resulted from differential bird predation giving an advantage to the melanistic phenotype in polluted regions, but not in unpolluted regions where the light coloured *typica* moths had the advantage. Various experiments have been performed on predation of the peppered moth and each has supported this hypothesis.

The most famous experiments on the peppered moth were carried out by Bernard Kettlewell under the supervision of E. B. Ford, who helped him gain a grant from the Nuffield Foundation to perform the experiments. In one of Kettlewell's experiments, moths were released into a large (18 m by 6 m) aviary, where they were fed on by Great Tits (*Parus major*). In 1953, Kettlewell experimented at Cadbury Nature Reserve in Birmingham, England, marking, releasing and recapturing marked moths. He found that in this polluted woodland *typica* morphs were preferentially preyed. He thus showed that the melanistic phenotype was important to the survival of peppered moths in such a habitat. Kettlewell repeated the experiment in 1955 at unpolluted woodland in Dorset and again in the polluted woods in Birmingham. He was accompanied by Nico Tinbergen, and they made a film together. Further studies by others found similar results, culminating in 1996 when reporting work on both sides of the Atlantic found a correlation between changes in melanic frequencies and pollution levels.

An experiment in field biology will always suffer from some level of artificiality, but that has to be balanced against practicality, costs and in this case the history of field biology; the most important aspect is that an experiment generates useful statistics. The only previous experiments of this type were R.A. Fisher and E.B. Ford's (1947) with the scarlet tiger moth.

Michael Majerus in his 1998 book *Melanism: Evolution in Action* discussed criticisms concerning Kettlewell's experimental methods. Criticism and controversy arose when the book was misrepresented in reviews, and the story was picked up by creationist campaigners. The journalist Judith Hooper suggested in her book *Of Moths and Men* (2002) that Kettlewell committed scientific fraud. Careful studies of Kettlewell's surviving papers by Rudge (2005) and Young (2004) have revealed that Hooper's allegation of fraud is unjustified, and "that Hooper does not provide one shred of evidence to support this serious allegation”.

In 2000 Majerus developed plans for experiments to establish where peppered moths rest through the day, and to examine if the various valid criticisms of Kettlewell’s experimental protocols could have altered the qualitative validity of his conclusions. In the following year he piloted a new field predation experiment designed to overcome criticisms that Kettlewell had used too few release sites, resulting in the density of moths being too high; moths had been released onto tree trunks rather than branches; moths released during the day might not have found the best places to hide; mixtures of wild-caught and lab-bred moths might have behaved differently; and the behaviour of translocated moths might have changed because of local adaptation. During the main experiment in Cambridge over the seven years 2001-2007 Majerus noted the natural resting positions of the moths, and of the 135 moths examined over half were on tree branches, mostly on the lower half of the branch, 37% were on tree trunks, mostly on the north side, and only 12.6% were resting on or under twigs. Following correspondence with Hooper he added an experiment to find if bat predation might have skewed the results – this found that bats preyed equally on both forms of the moth. He observed a number of species of bird preying on the moths, and the overall data led him to conclude that differential bird predation was a major factor responsible for the decline in *carbonaria* frequency compared to *typica* in Cambridge during the study period. He described his results as a complete vindication of the peppered moth story, and said "If the rise and fall of the peppered moth is one of the most visually impacting and easily understood examples of Darwinian evolution in action, it should be taught. It provides after all the proof of evolution."

Alternative hypotheses

Several alternative hypotheses to explain industrial melanism, particularly noted in the peppered moth, were proposed during the 1920s and 1930s. Some dissenters within the scientific community have criticized the peppered moth story, notably Sargent *et al.* (1998), but peppered moth researchers remain unconvinced.

Several alternative selection mechanisms have been proposed. Note that a change in allele frequency, be it caused by natural selection, mutation, migration or genetic drift by definition, is differential. However, the magnitude of the changes observed can only be accounted for by natural selection. It can be seen from population genetics that a non-differential change will not cause evolution. If the allele frequencies are denoted by the algebraic terms p and q, and (say) $p = 0.6$ and $q = 0.4$, then a non-differential reduction in population size from say 2000 to 100 individuals, will still produce the same values of (approximately) $p = 0.6$ and $q = 0.4$.

Phenotypic induction

John William Heslop-Harrison (1920) rejected Tutt's differential bird predation hypothesis, on the basis that he did not believe that birds ate moths. Instead he advocated the idea that pollutants could cause changes to the soma and germ plasm of the organism. The origin of this hypothesis probably has its roots in the 1890s, when it was proposed as a form of Lamarckism. It is important to note its historical context.

Hasebroek (1925) was the first who tried to prove this hypothesis, he contended that air pollution altered lepidopteran physiology, thus producing an excess of black pigment. He exposed pupae of Lepidoptera to various doses of pollutant gases, namely hydrogen sulfide (H_2S), ammonia (NH_3) and "pyredin" (presumably his spelling of pyridine). He used eight species in his studies, four of which were species of butterfly that did not exhibit melanism. Ford (1964) contends that Hasebroek's illustrations showed that the abnormal forms that appeared were not melanics, and Hasebroek failed to study their genetics.

Heslop Harrison (Harrison and Garrett 1926; Harrison 1928) suggested that the increase of melanic moths in industrialised regions was due to "mutation pressure", not to selection by predators which he regarded as negligible. Salts of lead and manganese were present in the airborne pollutant particles, and he suggested that these caused the mutation of genes for melanin production but of no others. He used *Selenia bilunaria* and *Tephrosia bistortata* as material. The larvae were fed with leaves that had incorporated these salts and melanics subsequently appeared.

Similar experiments by Hughes McKenney (1932) and Thomasen and Lemche (1933) failed to replicate these results. However, the statistician and geneticist Ronald Fisher, showed that Heslop Harrison's controls were inadequate. This hypothesis, however, appeared to be falsified by breeding experiments. Further evidence, if it were needed, is likely to come from research into the biochemistry of melanism.

Criticism and controversy

Creationists have disputed the occurrence or significance of the melanic *carbonaria* morph increasing in frequency.

In recent years, the use of the peppered moth as an example of evolution has come under attack by advocates of intelligent design and other creationists, who allege that it is not reliable as evidence of evolution.

Creationists have argued that the "peppered moth story" showed only microevolution, rather than speciation or other changes at the larger macroevolutionary scale. Biologists agree that this example shows natural selection causing evolution within a species, demonstrating rapid and obvious adaptiveness with such change, and accept that it is not proof of the theory of evolution as a whole. However, though creationists accept "microevolution" of varieties within a "kind", they claim that "macroevolution" does not happen. To biologists there is no dividing line between the two, and in the modern evolutionary synthesis the same mechanisms are seen operating at various scales to cause both evolution within species and speciation at a macroevolution level or wider changes, the only difference being of time and scale.

Another common, but unfounded, criticism involves well-known pictures of moths resting on trunks, used in many textbooks. These photos were prepared (dead moths pinned to branches), which has been conflated into the idea that all the studies were staged, ignoring the point that professional photography to illustrate textbooks uses dead insects because of the considerable difficulty in getting good images of small, relatively fast moving, animals, and that the studies actually consisted of observational data rather than using such photographs. The photographs in Michael Majerus's 1998 book

Melanism: Evolution in Action are unstaged pictures of live moths in the wild, and the photographs of moths on tree-trunks, apart from some slight blurring, look no different than the "staged" photographs.

Furthermore, while an experiment did involve the gluing of dead moths to trees, this practice was just one of many different ways used to study different individual elements of the overall hypothesis. This particular experiment was not meant to exactly reproduce natural conditions, but instead was used to assess how the numbers of moths available (their density) affected the foraging practices of birds.

The methodology of Bernard Kettlewell's classic study was questioned in a review by the biologist Jerry Coyne in *Nature* of Michael Majerus's 1998 book *Melanism: Evolution in Action* which includes a critique of Kettlewell's experiment, matching a similar 1998 analysis by Sargent *et al.* Coyne stated that the most serious problem found by Majerus was that only two peppered moths had been found on tree trunks. He also noted that the white moths had increased in numbers before the lichen had returned, and that Kettlewell's findings of moths choosing matching backgrounds had not been replicated in later experiments. Coyne compared his reaction to "the dismay attending my discovery, at the age of 6, that it was my father and not Santa who brought the presents on Christmas Eve". He concluded that "for the time being we must discard *Biston* as a well-understood example of natural selection in action, although it is clearly a case of evolution. There are many studies more appropriate for use in the classroom", and that further studies of the animal's habits were needed. At the beginning of his second paragraph on the peppered moths, Majerus emphasises that the wealth of additional data obtained since Kettlewell's initial predation papers does not undermine the basic qualitative deductions from that work, and that differential bird predation of the dark and light moths in habitats affected by industrial pollution to different degrees (directional selection) "is the primary influence of the evolution of melanism in the peppered moth". Coyne had erred in his statement that only two peppered moths had been found on tree trunks, as the book gives the resting positions of 47 peppered moths Majerus had found in the wild between 1964 and 1996; twelve were on tree trunks (six exposed, six unexposed), twenty were at the trunk/branch joint, and fifteen resting on branches. Majerus found that the review did not reflect the factual content of the book or his own views, and cites an assessment by the entomologist Donald Frack that there was essentially no resemblance between the book and Coyne's review, which appeared to be a summary of the Sargent et al. paper rather than Majerus's book.

The review was subsequently picked up by journalist Robert Matthews, who wrote an article for *The Sunday Telegraph*, March 14, 1999, claiming that "Evolution experts are quietly admitting that one of their most cherished examples of Darwin's theory, the rise and fall of the peppered moth, is based on a series of scientific blunders. Experiments using the moth in the Fifties and long believed to prove the truth of natural selection are now thought to be worthless, having been designed to come up with the 'right' answer". Majerus regarded this view as surprising, and not one that would be shared by those involved in the field. He stated that he had spoken to Matthews for over half an hour and had to explain many details as Matthews hadn't read the book, but "Even then, he got nearly everything wrong."

The story was taken up by creationists, and at a seminar presenting his wedge strategy on March 13, 1999, the leading intelligent design proponent Phillip E. Johnson asserted that the moths "do not sit on tree trunks", "moths had to be glued to the trunks" for pictures and that the experiments were "fraudulent" and a "scam." This led Frack to exchanges with intelligent design proponent Jonathan Wells, who conceded that Majerus listed six moths on exposed tree trunks (out of 47), but argued that this was "an insignificant proportion". Wells wrote an essay on the subject, a shortened version of which appeared in *The Scientist* of May 24, 1999, claiming that "In 25 years of fieldwork, C.A. Clarke and his colleagues found only one peppered moth on a tree trunk", and concluding that "The fact that peppered moths do not normally rest on tree trunks invalidates Kettlewell's experiments". In 2000 he wrote *Icons of Evolution: Why much of what we Teach About Evolution is Wrong*, which claims "What the textbooks don't explain, however, is that biologists have known since the 1980s that the classical story has some serious flaws. The most serious is that peppered moths in the wild don't even rest on tree trunks. The textbook photographs, it turns out, have been staged." The arguments put by Wells have been dismissed by Majerus, Cook and peppered moth researcher Bruce Grant who describes Wells as distorting the picture by selectively omitting or scrambling references in a way that is basically dishonest.

On November 27, 2000, the school board of Pratt County, Kansas continued efforts to favor intelligent design teaching by requiring the use of specific resources. These included by Jerry Coyne, who wrote to object strongly to this creationist misrepresentation of his critical re-evaluation, emphasising that the moth story is a sound example of evolution produced by natural selection and stating that his call for additional research was only to resolve uncertainty regarding bird predation as the cause of the natural selection and evolutionary change. Bruce Grant also wrote to challenge allegations of fraud in the moth experiments based on misrepresentations by Wells.

In 2002, Judith Hooper's *Of Moths and Men* added to the chorus of accusations of scientific fraud. She accused Kettlewell of manipulating his data to prove his hypothesis. The book received strong criticism from the scientific press (e.g., Coyne, B.C. Clarke, Grant). Majerus described it as "littered with errors, misrepresentations, misinterpretations and falsehoods".

Chapter- 6

Sexual Selection

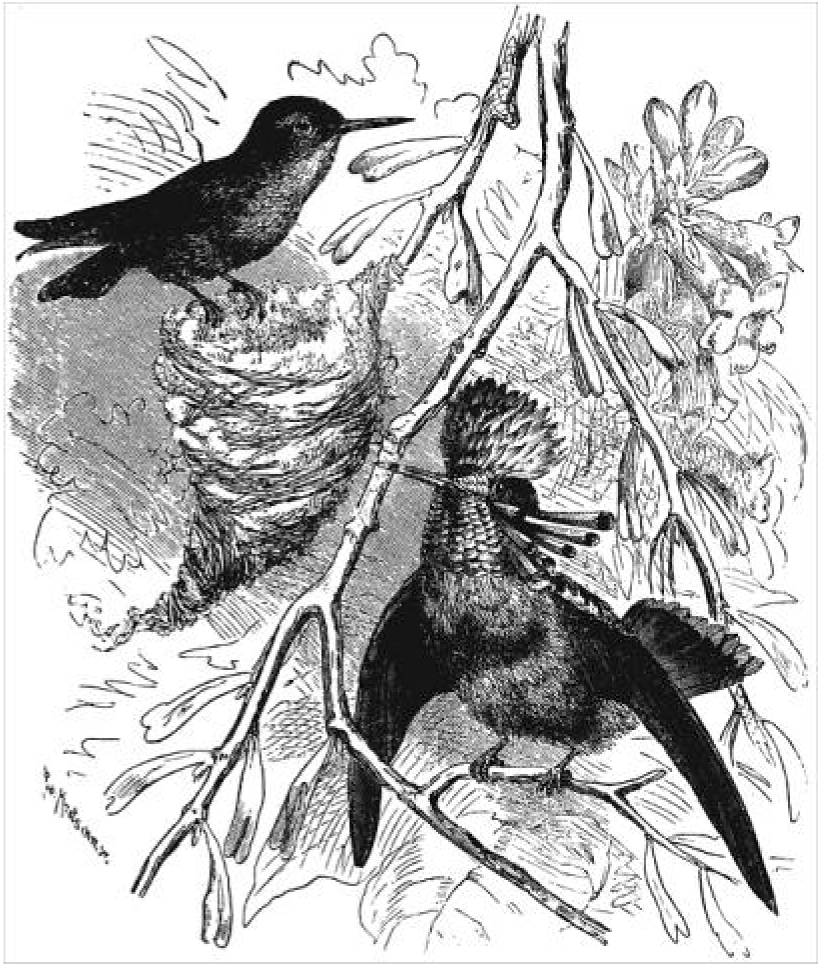
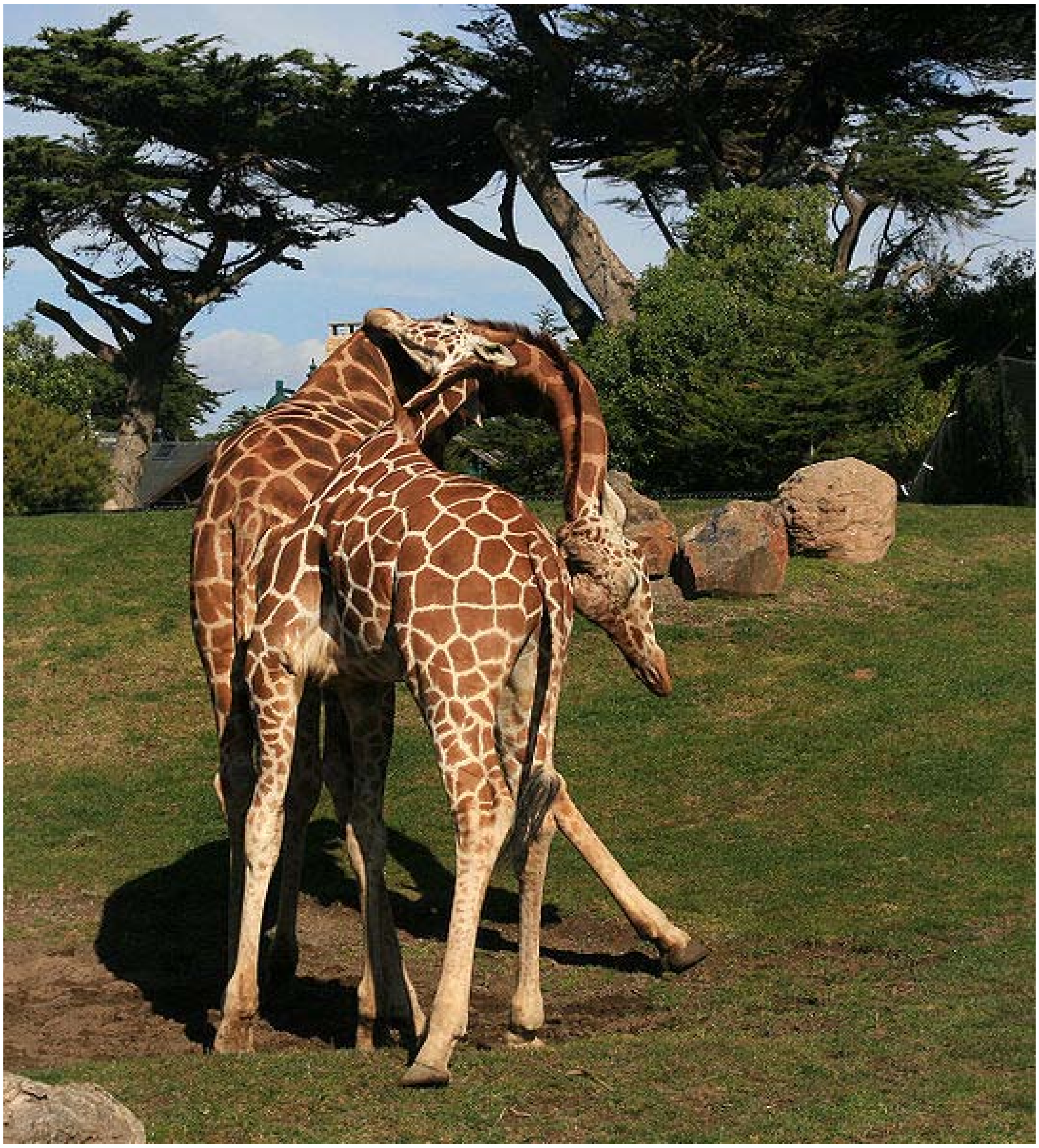


Illustration from *The Descent of Man and Selection in Relation to Sex* by Charles Darwin showing the Tufted Coquette *Lophornis ornatus*, female on left, ornamented male on right.

Sexual selection is the theory proposed by Charles Darwin that states that certain evolutionary traits can be explained by intraspecific competition. Darwin defined sexual selection as the effects of the "struggle between the individuals of one sex, generally the males, for the possession of the other sex". Biologists today distinguish between "male to male combat" or "Intrasexual Selection" (it is usually males that fight each other), "mate choice" or "Intersexual Selection" (usually female choice of male mates) and sexual conflict. Traits selected by male combat are called secondary sexual characteristics (including horns, antlers, etc.) and sometimes referred to as "weapons"; and traits selected by mate choice are called "ornaments". Much attention has been given to *cryptic* female choice, a phenomenon in internally fertilising animals such as mammals and birds, where a female will get rid of a male's sperm without his knowledge. The equivalent in male-to-male combat is sperm competition.

Females often prefer to mate with males with external ornaments, exaggerated features of morphology. These preferences may arise when an arbitrary female preference for some aspect of male morphology—initially increased by genetic drift—creates, in due course, selection for males with the appropriate ornament. This is known as the sexy son hypothesis. Alternatively, genes that enable males to develop impressive ornaments or fighting ability may simply show off greater disease resistance or a more efficient metabolism, features that also benefit females. This idea is known as the good genes hypothesis.

Phylogeny of sexual selection and base conditions



Two male Giraffes,*Giraffa camelopardalis reticulata* necking in San Francisco Zoo.

The success of an organism is not only measured by the number of offspring left behind, but by the quality or probable success of the offspring: reproductive fitness. Sexual selection is the expansion on the ability of organisms to differentiate each other at the *species* level, inter*species* selection.

> “The grossest blunder in sexual preference, which we can conceive of an animal making, would be to mate with a species different from its own and with which hybrids are either infertile or, through the mixture of instincts and other attributes appropriate to different courses of life, at so serious a disadvantage as to leave no descendants. ..it is no conjecture that a discriminative mechanism exists, variations in which will be capable of giving rise to a similar discrimination within its own species, should such a discrimination become at any time advantageous. — *Ronald Fisher, 1930*”

The expansion of interspecies selection and intraspecies selection is a driving force behind species fission: the separation of a single contiguous species into multiple non-contiguous variants. Sexual preference creates a specialized tendency towards homogamy that provides a system by which a group constantly invaded by the diffusion of unfavourable genes may suppress ill effects.

> “Individuals in each region most readily attracted to or excited by mates of the type there favored, in contrast to possible mates of the opposite type, will, in fact, be the better represented”

> in future generations, and both the discrimination and the preference will thereby be enhanced. It appears certainly possible that an evolution of sexual preference due to this cause would establish an effective isolation between two differentiated parts of a species, even when geographical and other factors were least favorable to such separation. —*Ronald Fisher, 1930*

When it is possible for it to be exercised usefully, the general conditions of sexual discrimination appear to be (1) the acceptance of one mate precludes the effective acceptance of alternative mates, and (2) the rejection of an offer will be followed by other offers, either certainly, or at such high chance that the risk of non-occurrence will be smaller than the chance advantage to be gained by selecting a mate.

Intrasexual and intersexual selection

Male Northern Elephant Seals fight fiercely each year. Unsuccessful males might not mate at all, while successful males have harems of 30 to 100 females.

Sexual selection takes two major forms: intrasexual selection (also known as 'male–male competition') in which members of the less limited sex (typically males) compete aggressively among themselves for access to the limiting sex, and intersexual selection (also known as 'mate choice' or 'female choice') in which males compete with each other to be chosen by females.

> “ The sexual struggle is of two kinds: in the one it is between the individuals of the same sex, generally the males, in order to drive away or kill their rivals, the females remaining passive; while in the other, the struggle is likewise between the individuals of the same sex, in order to excite or charm those of the opposite sex, generally the females, which no longer remain passive, but select the more agreeable partners. —*Charles Darwin, 1871* ”

With **intrasexual selection** it should be brought to mind that adorned males will gain reproductive advantage without the intervention of female preference and intersexual selection. This advantage will be conferred by weapons used in the process of resolving disputes, such as those over territorial rights. The use of male sexual ornamentation is primarily used in the search of asymmetries between rival males, contrary to what would seem most obvious (mortally wounding the opponent), since a high number of fatal combats over territory would result in a clear disadvantage. The use of sexual ornamentation is used as a signaling device (signalling theory) amongst males to create a dominance hierarchy, also known as a pecking order, without unneeded detriment and fatality. It is predominantly when two opposing males are so closely matched, as would be found in males not having established themselves in a dominance hierarchy, that asymmetries cannot be found and the confrontation escalates to a point where the asymmetries must be proved by aggressive use of ornamentation.

> “ As a propagandist the cock behaves as though he knew that it was advantageous to impress the males as the females of his species, and a sprightly bearing with fine feathers and triumphant song are quite as well adapted for war-propaganda as for courtship. —*Ronald Fisher, 1930* ”

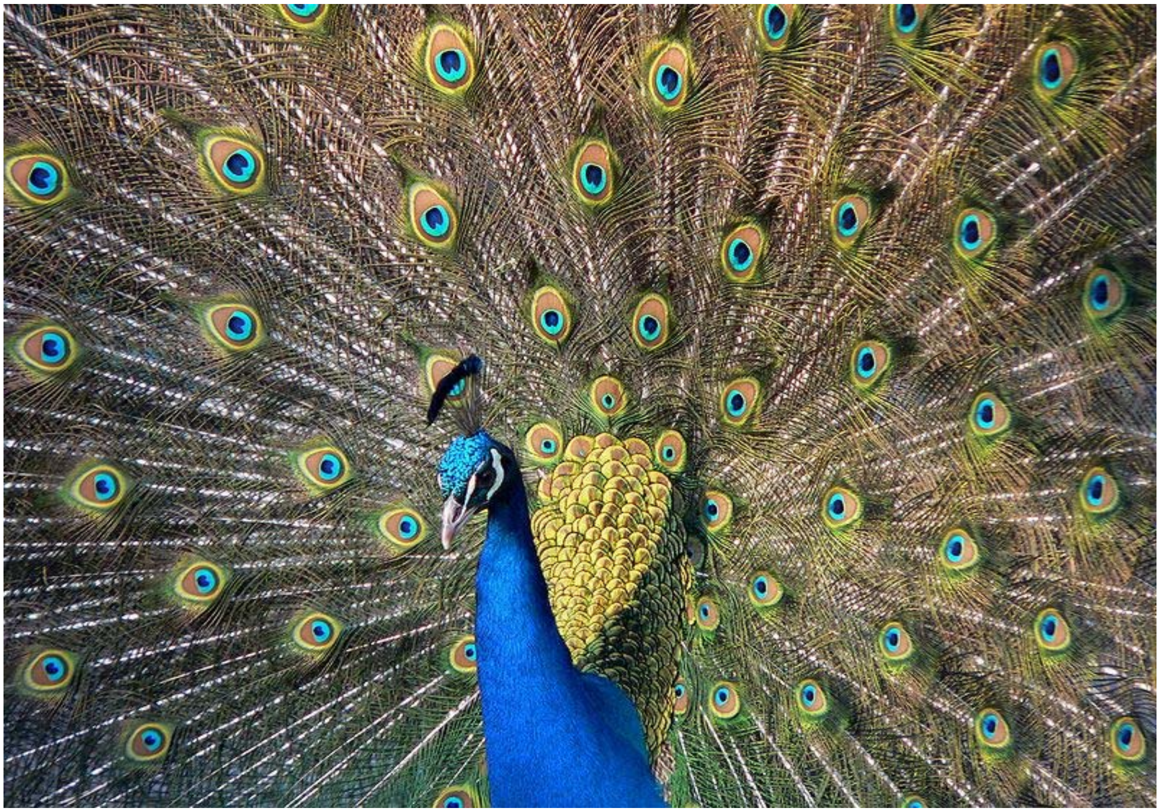
How often males will physically engage each other, and in what manner, can best be understood by applying game theory developed for biology, most notably by John Maynard Smith.

In addition to conventional aggression, male–male competition may take the form of sperm competition.

However, 'sexual selection' typically refers to the process of choice (the limiting factor, which is typically females) over members of the opposite sex (the non-limited factor, typically males). This process is known as **intersexual selection**. Fisher pointed out that preference could be under genetic control and therefore subject to a combination of natural and sexual selection just as much as the qualities of the ornamentation 'preferred'.

The conditions determining which sex is the limiting factor in intersexual selection can be best understood by way of Bateman's principle which states that *the sex which invests* *the most in producing offspring becomes a limiting resource over which the other sex will compete.* This can be most easily illustrated by the contrast in nutritional investment into a zygote between egg and sperm, and the limited reproductive capacity of females compared to males.

Geometric progression



An example of intersexual selection: the female peahen chose to mate with the male peacock that, in her mind, had the most beautiful plumage.

In species where the reproductive success of one sex depends heavily on winning the concession of the other, as with many polygamous birds, sexual selection will act by increasing the degree of preference to which it is due, with the consequence that both the trait preferred and the intensity of preference will be increased together. This process causes a fervent and rapid evolution of both the conspicuous ornamentation and the preference for such, until arrested directly or indirectly for ecological reasons. Thus, in many cases a positive feedback loop of sexual selection is created, resulting in exorbitant physical structures in the non-limited sex, the most notorious example being the peacock (shown above). It is important to note that while a peacock may have exorbitant plumage, the peahen has even more exorbitant taste for such.

Initially to start the process there would need to be a correlation between the trait and higher fitness. For this example we use a hypothetical species of songbird, of the order

Passeriformes. Tail length in these birds is correlated with fitness such that longer tails equate to higher fitness. As females of subsequent generations favor males with longer tails, the preference for them would cause them to be conspicuously favored after many generations.

The peahen will desire to mate with the most attractive Peacock so that her progeny, if male, will be attractive to females in the next generation. Additionally the Peacock will desire to mate with a Peahen that finds him attractive so that if the progeny is female, preference for his degree of ornamentation remains present in the next generation. Since the rate of change in preference is proportioned according to the highest average degree of taste amongst females, and that females desire to best other members of the sex, it creates an additive effect in the cyclical process that will yield exponential increases, in both sexes, if unchecked.

R.A.Fisher in The Genetical Theory of Natural Selection was the first to articulate this process in a game theoretic style treatment.

> “ plumage development in the male, and sexual preference for such developments in the female, must thus advance together, and so long as the process is unchecked by severe counterselection, will advance with ever-increasing speed. In the total absence of such checks, it is easy to see that the speed of development will be proportional to the development already attained, which will therefore increase with time exponentially, or in geometric progression. —*Ronald Fisher, 1930* ”

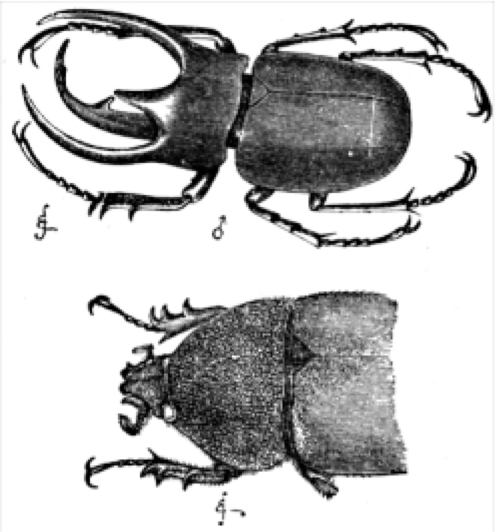
> “ The exponential element, which is the kernel of the thing, arises from the rate of change in hen taste being proportional to the absolute average degree of taste. —*Ronald Fisher, 1932* ”

> “ It is important to notice that the conditions of relative stability brought about by these or other means, will be far longer duration than the process in which the ornaments are evolved. In most existing species the runaway process must have been already checked, and we should expect that the more extraordinary developments of sexual plumage are not due like most characters to a ”

> long and even course of evolutionary
> progress, but to sudden spurts of change. —
> *Ronald Fisher, 1930*

Since Fisher's initial conceptual model of the 'run-away' process, various others have continued the work on modeling an accurate mathematical proof. Notably R.Lande & P.O'Donald.

Sexual dimorphism



The Stag beetle demonstrates a classic case of sexual dimorphism. This plate is from Darwin's *Descent of Man*, with the male at top, female at bottom.

Sex differences directly related to reproduction and serving no direct purpose in courtship are called primary sexual characteristics. Traits amenable to sexual selection, which give an organism an advantage over its rivals (such as in courtship) without being directly involved in reproduction, are called secondary sex characteristics.

In most sexual species the males and females have different equilibrium strategies, due to a difference in relative investment in producing offspring. As formulated in Bateman's principle, females have a greater initial investment in producing offspring (pregnancy in mammals or the production of the egg in birds and reptiles) , and this difference in initial investment creates differences in variance in expected reproductive success and bootstraps the sexual selection processes. Classic examples of reversed sex-role species include the pipefish, and Wilson's phalarope. Also, unlike a female, a male (except in monogamous species) has some uncertainty about whether or not he is the true parent of a child, and so will be less interested in spending his energy helping to raise offspring that may or may not be related to him. As a result of these factors, males are typically more willing to mate than females, and so females are typically the ones doing the choosing (except in cases of forced copulations, which can occur in certain species of primates, ducks, and others). The effects of sexual selection are thus held to typically be more pronounced in males than in females.

Differences in secondary sexual characteristics between males and females of a species are referred to as sexual dimorphisms. These can be as subtle as a size difference (sexual size dimorphism, often abbreviated as SSD) or as extreme as horns and color patterns. Sexual dimorphisms abound in nature. Examples include the possession of antlers by only male deer, and the brighter coloration of many male birds, in comparison with females of the same species. The peacock, with its elaborate and colorful tail feathers, which the peahen lacks, is often referred to as perhaps the most extraordinary example of a dimorphism. The largest sexual size dimorphism in vertebrates is the shell dwelling cichlid fish *Neolamprologus callipterus* in which males are up to 30 times the size of females. Extreme sexual size dimorphism, with females larger than males, is quite common in spiders.

Viability and variations of the theory

Due to their sometimes greatly exaggerated nature, secondary sexual characteristics can prove to be a hindrance to an animal, thereby lowering its chances of survival. For example, the large antlers of a moose are bulky and heavy and slow the creature's flight from predators; they also can become entangled in low-hanging tree branches and shrubs, and undoubtedly have led to the demise of many individuals. Bright colorations and showy ornamenations, such as those seen in many male birds, in addition to capturing the eyes of females, also attract the attention of predators; when a male peacock spreads its tail, it is beautiful, but very obvious (though this may actually be advantageous to the survival of the male's offspring and the breeding population as a whole; see below). Some of these traits also represent energetically costly investments for the animals that bear them. Because traits held to be due to sexual selection often conflict with the survival fitness of the individual, the question then arises as to why, in nature, in which survival of the fittest is considered the rule of thumb, such apparent liabilities are allowed to persist.

An often-cited theory published by R.A. Fisher in 1930 that attempts to resolve the paradox posits that such traits are the results of explosive positive feedback loops that have as their starting points particular sexual preferences for features that confer a survival advantage and thus "become established in the species." Fisher argued that such features advance in the direction of the preference even beyond the optimal level for survival, until the selection pressure of female choice is precisely counterbalanced by the resultant disadvantage for survival. Fisher further argued that the strength of the female preference tends to grow exponentially (leading to 'explosive' evolution of the characteristic) until finally checked by ecological selection, since the offspring of those females with the strongest preference typically fare better in reproducing than the offspring of females with weaker preferences. Any mutations for the preference opposite to the given characteristic, though tending to promote survival against ecological selection, nevertheless tend not to survive in the gene pool because male offspring that result from matings based on the preference are less sexually attractive to the majority of the females in the population, and thus infrequently chosen as mates. An equivalent way of expressing this is that if most females are looking, for example, for long-tailed males, then each female individually does better to select a long-tailed male, since then her male children are more likely to succeed. (The females do not actually have this thought process; this kind of "decision" is an evolutionarily stable strategy.)

Other theories highlight intrinsically useful qualities of such traits. Antlers, horns and the like can be used in physical defense from a predator, and also in show jousting or competition among males in a species. The winner, which typically becomes the dominant animal in the population, is granted access to females, and therefore increases his reproductive output. Antlers are not the only mechanism that can be used to counteract predation. Predators typically look for the eyes of their prey so they can attack that end of the creature. The conspicuousness of eyespots on many species of butterflies and fishes confuses predators and helps to prevent the prey from suffering serious damage.

Another, more recently developed, theory, the Handicap principle of Amotz Zahavi, Russell Lande and W. D. Hamilton, holds that the fact that the male of the species is able to survive until and through the age of reproduction with such a seemingly maladaptive trait is effectively considered by the female to be a testament to his overall fitness. Such handicaps might prove he is either free of or resistant to disease, or it might demonstrate that this animal possesses more speed or a greater physical strength that is used to combat the troubles brought on by the exaggerated trait.

Zahavi's work spurred a re-examination of the field, which has produced an ever-accelerating number of theories. In 1984, Hamilton and Marlene Zuk introduced the "Bright Male" hypothesis, suggesting that male elaborations might serve as a marker of health, by exaggerating the effects of disease and deficiency. In 1990, Michael Ryan and A.S. Rand, working with the túngara frog, proposed the hypothesis of "Sensory Exploitation", where exaggerated male traits may provide a sensory stimulation that females find hard to resist. In 1991, Anders Pape Møller, working with the tails of male barn swallows, introduced fluctuating asymmetry to the field. Fluctuating asymmetry, a concept previously invoked under natural selection, is based on the observations that healthier specimens have more left-to-right sided symmetry than less healthy specimens. Subsequently the theories of the "Gravity Hypothesis" by Jordi Moya-Larano et al. and "Chase Away" by Brett Holland and William R. Rice have also been added. In addition, in the late 1970s Janzen and Mary Willson, noting that male flowers are often larger than female flowers, expanded the field of sexual selection into plants.

In the past few years, the field has exploded to include many additional areas of study, not all of which are clearly included under Darwin's definition of sexual selection. These include cuckoldry, nuptial gifts, sperm competition, infanticide, physical beauty, mating by subterfuge, species isolation mechanisms, male parental care, ambiparental care, mate location, polygamy, and mechanisms that can only be called bizarre, including homosexual rape in certain male animals, cementing of females' vaginal pores by males in some lepidopteran insects, and insect penises specialized to remove any sperm packets from females which may have been deposited by previous suitors.

These theories are not mutually exclusive; combinations of them may also be considered.

Focusing on the effect of sexual conflict, as hypothezised by William Rice, Locke Rowe et Göran Arnvist, Thierry Lodé underlines that the divergence of interest constitutes a key for evolutionary process. Sexual conflict leads to an antagonistic co-evolution in which one sex tends to control the other, resulting in a tug of war. Besides, *the sexual propaganda theory* only argued that mate were opportunistically lead, on the basis of various factors determining the choice such as phenotypic characteristics, apparent vigor of individual, strength of mate signals, trophic resources, territoriality etc and could explain the maintenance of genetic diversity within populations.

In humans

Charles Darwin conjectured that the male beard, as well as the relative hairlessness of humans compared to nearly all other mammals, are results of sexual selection. He reasoned that since, compared to males, the bodies of females are more nearly hairless, hairlessness is one of the atypical cases due to its selection by males at a remote prehistoric time, when males had overwhelming selective power, and that it nonetheless affected males due to genetic correlation between the sexes. He also hypothesized that sexual selection could also be what had differentiated between different human races, as he did not believe that natural selection provided a satisfactory answer.

Geoffrey Miller, drawing on some of Darwin's largely neglected ideas about human behavior, has hypothesized that many human behaviors not clearly tied to survival benefits, such as humor, music, visual art, verbal creativity, and some forms of altruism, are courtship adaptations that have been favored through sexual selection. In that view, many human artefacts could be considered subject to sexual selection as part of the extended phenotype, for instance clothing that enhances sexually selected traits.

Some hypotheses about the evolution of the human brain argue that it is a sexually selected trait, as it would not confer enough fitness in itself relative to its high maintenance costs (a quarter to a fifth of the energy and oxygen consumed by a human). Related to this is vocabulary, where humans, on average, know far more words than are necessary for communication. Miller (2000) has proposed that this apparent redundancy is due to individuals using vocabulary to demonstrate their intelligence, and consequently their “fitness”, to potential mates. This has been tested experimentally and it appears that males do make greater use of lower frequency (more unusual) words when in a romantic mindset compared to a non-romantic mindset, meaning that vocabulary is likely to be used as a sexual display (Rosenberg & Tunney, 2008).

The evolutionary biologist Richard Dawkins has speculated that the loss of the penis bone in humans, when it is present in other primates, may be due to sexual selection by females looking for an honest advertisement of good health in prospective mates. Since a human erection relies on a hydraulic pumping system, erection failure is a sensitive early warning of certain kinds of physical and mental ill health.

History and application of the theory

Victorian cartoonists quickly picked up on Darwin's ideas about the role of display in sexual selection. Here Darwin is fascinated by the apparent steatopygia in the new fashion for bustles. The woman asks him to "leave my emotions alone", a reference to Darwin's new book *The Expression of the Emotions in Man and Animals*.

The theory of sexual selection was first proposed by Charles Darwin in his book *The Origin of Species*, though it was primarily devoted to natural selection. A later work, *The Descent of Man and Selection in Relation to Sex* dealt with the subject of sexual selection exhaustively, in part because Darwin felt that natural selection alone was unable to account for certain types of apparently non-competitive adaptations, such as the tail of a male peacock. He once wrote to a colleague that "The sight of a feather in a peacock's tail, whenever I gaze at it, makes me sick!" His work divided sexual selection into two primary categories: male-male competition (which would produce adaptations such as a Bighorn Sheep's horns, which are used primarily in sparring with other males over females), and cases of female choice (which would produce adaptations like beautiful plumage, elaborate songs, and other things related to impressing and attracting).

Darwin's views on sexual selection were opposed strongly by his "co-discoverer" of natural selection, Alfred Russel Wallace, though much of his "debate" with Darwin took place after Darwin's death. Wallace argued that the aspects of it which were male-male competition, while real, were simply forms of natural selection, and that the notion of "female choice" was attributing the ability to judge standards of beauty to animals far too cognitively undeveloped to be capable of aesthetic feeling (such as beetles).

Wallace also argued that Darwin too much favored the bright colors of the male peacock as adaptive without realizing that the "drab" peahen's coloration is itself adaptive, as camouflage. Wallace more speculatively argued that the bright colors and long tails of the peacock were *not* adaptive in any way, and that bright coloration could result from non-adaptive physiological development (for example, the internal organs of animals, not being subject to a visual form of natural selection, come in a wide variety of bright colors). This has been questioned by later scholars as quite a stretch for Wallace, who in this particular instance abandoned his normally strict "adaptationist" agenda in asserting that the highly intricate and developed forms such as a peacock's tail resulted by sheer "physiological processes" that were somehow not at all subjected to adaptation.

Though Darwin considered sexual and natural selection to be two separate processes of equal importance, most of his contemporaries were not convinced, and sexual selection is usually de-emphasized as being a lesser force than, or simply a part of, natural selection.

The sciences of evolutionary psychology, human behavioral ecology, and sociobiology study the influence of sexual selection in humans, though these are often controversial fields. The field of epigenetics is broadly concerned with the competence of adult organisms within a given sexual, social, and ecological niche, which includes the development of mating competences, e.g., by mimicking adult behavior.

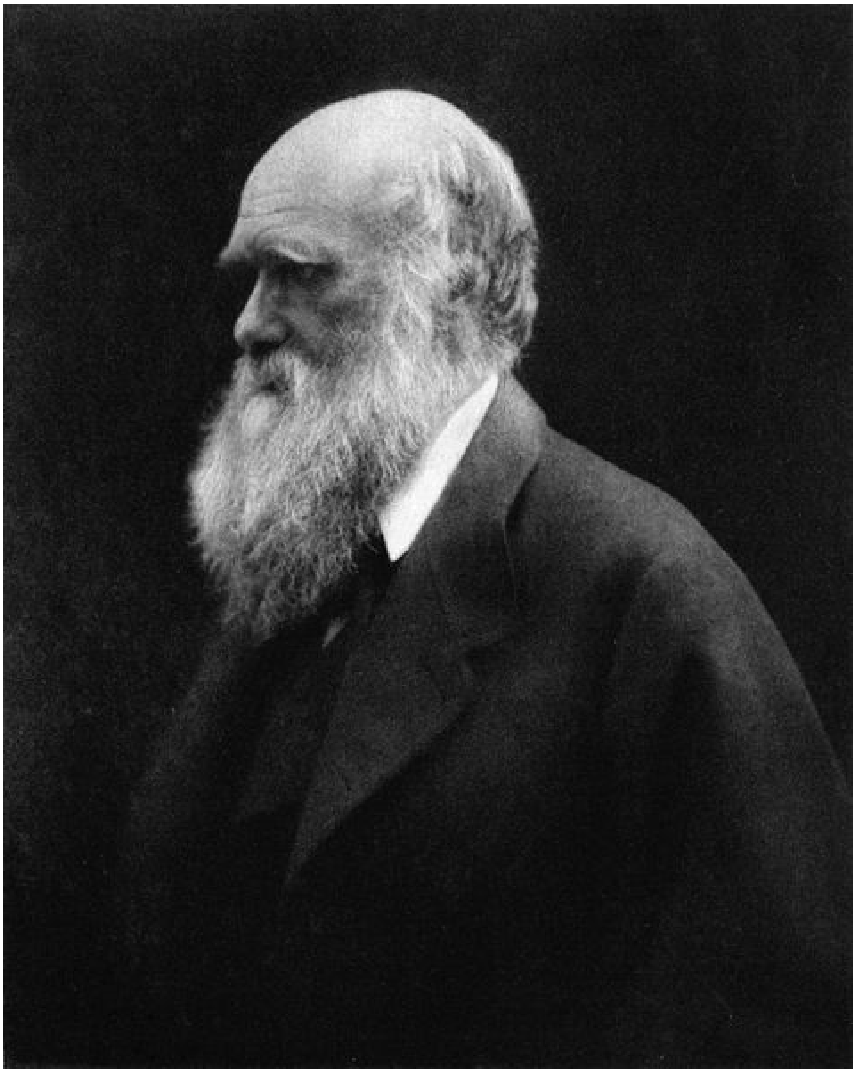
Criticism

Ecologist Joan Roughgarden criticised sexual selection in a 2006 paper and a follow-up book in 2009 claiming that individuals do not compete strongly for mating opportunities, proposing that the function of sex is mostly social. Sexual selection researchers and evolutionary theorists have heavily criticised these ideas, accusing Roughgarden of factual inaccuracy, unwarranted assumptions, and ignorance of recent research on sexual selection.

Cultural critics have also proposed that Darwin's ideas about sexual selection were strongly shaped by Victorian mores and may at times reflect a distinct chauvinistic bias.

Chapter- 7

Sexual Selection in Human Evolution



Charles Darwin conjectured that the male beard was the product of sexual selection in prehistoric times

Charles Darwin described sexual selection as depending "on the advantage that certain individuals have over others of the same sex and species solely in respect of reproduction". In animals he saw the competition for advantage as occurring between males; the most successful of which were chosen by females. However in humans Darwin came to think the evidence pointed toward male choice, he believed sexual selection could explain otherwise puzzling features of the human species including some aspects of appearance which vary geographically but seem to be trivial and superficial such as beards. It has been suggested that Darwin was attracted to understanding human evolution through a sexual selection hypothesis because he felt it upheld the unity of humankind against pro-slavery demagoguery by explaining how black people and white people had come to look unalike while emphasizing they were not separate species. Modern hypotheses which build on Darwin's ideas have mooted a geographical contrast in the intensity and direction of sexual selection between Europe and Africa. The general phenotypic differences between black people and white people are probably the result of both natural selection and sexual selection. Although skin color can be a target of sexual selection the skin color variation in humans is thought to be a result of natural selection along a latitude gradient.

Evolution of humans

Sexual dimorphism

Men are hairier than women and Darwin was of the opinion that hairlessness was related to sexual selection, however several other explanations have been advanced to explain human hairlessness, a leading one is loss of body hair to facilitate sweating. This idea dovetails with a suggested need for increased photoprotection and is part of the most commonly accepted scientific explanation for the evolution of pigmentary traits.

Sexual selection can be difficult to demonstrate as features may result from an equilibrium among competing selective pressures, some involving sexual selection, others natural selections. For example monogamous primates are known to typically exhibit little sexual dimorphism such as particularly large males armed with huge canines, however powerful big toothed males can provide protection against predators and may be bigger for that reason rather in order to win confrontations over females. Males and females differing in size can specialize in, and more fully exploit, different food resources while avoiding competing with each other, furthermore body size can be useful in avoiding predators and may also be of assistance in securing a mate - this is further complicated by the consideration that with larger body size the skeleton of mammals becomes much more robust and massive (relatively speaking). Bearing these caveats in mind levels of sexual dimorphism are generally seen as a marker of sexual selection, studies have shown the earliest homins were highly dimorphic and that this lessened over the course of the evolution of Homo, suggesting homins have became more monogamous.

A study found an evolutionary trend for men to have relatively shorter upper faces may have been caused by sexual selection on the simple ratio of upper face length to broadness as a proxy for facial attractiveness, possibly because women have preferred men who looked masculine but not aggressive. In an initial test calculations derived from the research were applied to photographs of male celebrities; Will Smith conformed most closely to the ideal proportions.

Darwin and more recent hypotheses

Charles Darwin conjectured that the male beard, as well as the hairlessness of humans compared to nearly all other mammals, are results of sexual selection. He reasoned that since the bodies of females are more nearly hairless the loss of fur was due to sexual selection of females at a remote prehistoric time when males had overwhelming selective power, and that it nonetheless affected males due to genetic correlation between the sexes. He also hypothesized that contrasts in sexual selection acting along with natural selection were significant factors in the geographical differentiation in human appearance of some isolated groups as he did not believe that natural selection alone provided a satisfactory answer. Although not explicit, his observation that in Khoisan women 'the posterior part of the body projects in a most wonderful manner' implies sexual selection for this characteristic. In the *Descent of Man*, Darwin viewed many physical traits which vary around the world as so trivial to survival that he concluded some input from sexual selection was required to account for their presence. He noted that variation in these features among the various peoples of the world meant human mate-choice criteria would also have to be quite different if the focus was similar and he himself doubted that citing reports indicating that ideals of beauty did not, in fact, vary in this way around the world. Sexual selection has continued to be suggested as a possible explanation for geographical variation in appearance within the human species, in modern hypotheses marriage practices are proposed as the main determinant of sexual selection. John Manning suggests where polygyny is common men face intense competition for wives and are more likely to be completely unsuccessful in reproducing, a result is strong selection of males for traits which are adaptive for successful reproduction. He proposes a link to skin color through selection of males for testosterone mediated traits which confer an ability to successfully compete for females and points to the fact that males have higher rates of many diseases as evidence that the effect of testosterone makes the human immune system less competent to resist pathogens. In this view the antimicrobial properties of melanin help mitigate the susceptibility to disease that polygyny induces by increasing testosteronization. Hence the anti-infective qualities of melanin were more important than protection from ultraviolet light in the evolution of the darkest skin types. Manning asserts that skin color is more correlated with the occurrence of polygyny - explicable by it having an anti microbial function - than the latitudinal gradient in intensity of ultraviolet radiation, he points to the lack of very dark skin at equatorial latitudes of the New World and the relatively light skin of Khoisan people in Africa.

Direction and intensity of sexual selection

Another proposed explanation for the evolution of pigmentary traits in humans though sexual selection is by Peter Frost who suggests European hair, eye, and skin color originated during the ice age when intense female-female rivalry for mates led to a series of adaptations for increased mating success. Modern research suggests that across a wide range of cultures a female face is seen as attractive if it has high eyebrows, widely spaced large eyes with dilated pupils, high cheekbones, a small nose, a narrow face with thin cheeks, a large smile, a full lower lip, a small chin, and a full hairstyle. Although these mate-choice criteria are largely universal the aesthetic preferences of men are constrained by the number of potential mates, without an excess to choose from there can be no overall selection.

Men are often unneeded during pregnancy and infant care and so they are usually free to serve the cause of maximizing their reproductive fitness though a return to the mate market; in practice many males will be competing for too few females at any one time. Males can best maximize their reproductive fitness (leave more descendants) in the tropics, there women relied least on men as providers - being able to gather fruits, vegetables, tubers, and eggs for themselves while still caring for infants. In higher latitudes however opportunities for food gathering are restricted and women tend to rely on their husband to provide for the family by hunting, consequently the cost of providing for a second wife makes polygyny impossible for all but the ablest hunters. Land supports fewer game animals per unit of land area at high latitude and hunting distance increases proportionately this makes hunters vulnerable to death by exposure, exhaustion, drowning, injuries and starvation.

These risks peak in the 'continental Arctic,' of steppe-tundra, an environment widespread in Europe during the Late Glacial Maximum. It is likely that those hunting mobile game animals on foot in this environment would have very high mortality. The death of many male providers allied to the fact that surviving men were unable to feed more than one wife may have meant a high proportion of women could never marry and reproduce; sexual selection of women for characteristics that would enable them to get a husband was intense. Studies show that recognition of objects does not proceed by attention to all features simultaneously; attention is initially directed to cues of 'brightness', 'colour' or shape'. Priority goes to the strikingly varied and vivid colors tend to be attributes of intense sexual selection. If mate competition is relatively weak, sexual selection focuses primarily on visible markers of mate quality which signify fecundity, as mate competition intensifies the focus will shift from functional to eye-catching novelty rather than biologic 'truth in advertising'.

With a glut of potential mates animals are swayed by eye-catching stimuli as when a secondary sexual characteristic is outsized or more vividly colored for effective hyperstimulating of the algorithms for sex-identification. Eyes and facial features that function in personal interaction and identification can be similarly highlighted. Brightly colored phenotypes can diversify under selection pressure into a polymorphism of phenotypes. Hair and eye pigmentation shows a remarkable diversity in Europe and frequency-dependent sexual selection *for* such diversity is a more likely explanation for it than any side effect of straightforwardly decreasing distribution of melanin following the latitudinal gradient of ultraviolet radiation.

Furthermore, the date of the mutations for the multitude of eye and hair colors found in Europe are closer to the late glacial maximum than when humans first entered Europe. Skin color dimorphism means that the characterization of women as the "fair sex" is in fact accurate; men have darker complexions in comparison to women as a result of differing melanin and hemoglobin levels in outer layers of the skin. Although this constitutive sex difference - which is not due to sun exposure - is less obvious in weakly pigmented peoples a hardwired mental mechanism enables us to recognize the gender of human faces.

The main clue to gender is complexion; people can distinguish a man's face from a woman's by the complexion and contrast between facial pigmentation and eye/lip pigmentation This slight - but significant - difference in pigmentation could explain why Europeans are white skinned. In premodern cultures there is a cross-cultural tendency to associate lighter skin with femininity and a preference for lighter skinned women as mates. In this way strong sexual selection of women is hypothesized to have altered the pigmentation of the entire population. The dating of the mutations for white skin and hair and eye colors are closer to the late glacial maximum than the original modern human entering of Europe as the UV-latitude hypothesis would presumably predict however, there are alternative, i.e. non-sexual selection, explanations for this (see below).

Criticism

The main critics of hypotheses which suggest that the extremes of skin pigmentation have resulted from sexual selection are those who see skin color as an *obvious* adaptation to excessive or inadequate ultraviolet radiation, they object that skin pigmentation accompanied loss of body hair while dark pigmentation evolved soon after the genus Homo in Africa, moreover a conspicuous latitude gradient of skin tones follows the out of Africa dispersion, these are conclusive. Therefore - it is argued - natural selection for sufficient ultraviolet penetration to enable vitamin D production while protecting folic acid gave rise to the evolution of skin pigmentation; light skin preference by males in some cultures may have - at most - slightly affected sexual dimorphism.

Indeed the case for human skin color as a adaptation to UV radiation is so clear an example of the mechanism of evolution by natural selection that it is a perfect model to demonstrate it. Deleterious health effects of insufficient vitamin D are also pointed to as confirmation that skin lightening was in response to strong selection pressure for maximizing vitamin D.

A variation of the vitamin D argument is has recently gained credence as awareness of the late dates for the origin of European specific skin, eye and hair lightening has grown and made an explanation for humans living in Europe for several thousand years without becoming white required.

The replacement of hunting by agriculture is claimed to have led to a dearth of vitamin D , therefore it was the elimination of game meat, fish, and some plants from the diet which resulted in skin turning white long after modern human settlement in Europe.

An anomaly for this conjecture is that if the consequence of switching from meat to an agricultural diet is skin becoming *less* pigmented then historically hunter gatherer population in Africa such as the Khoisan and Oromo peoples, who are *paler* than other sub Saharan Africans and basal to them, ought to have *darker* skin than historically agriculturist groups. However a leading proponent of the agriculturally caused pigmentation hypothesis maintains that sexual selection can not account for European pigmentation as it would have almost certainly have resulted in the traits of lighter skin, hair and eyes exhibiting strong sexual dimorphism.

Culture and sexual selection

Machiavellian models of Male-Male competition. In Highland New Guinea men 'know' that women secretly grow poisonous herbs. Young males want body fat and an oily skin because these are signs of strength. It is 'well known' contact with women depletes the strength of a male but semen increases it. Consequently male homosexuality rather than the exception, can be the norm. A possible explanation is the 'wise' males who convince the other younger men that women are dangerous are actually competing for access to females with the young males, by means of a deception strategy convincing the potentially rival males that women are enervating and polluting enables the deceiving male to access to women with less competition from the gullible believers. The promulgation of such canards is by senior males who may explain that they are already old and without strength so they are sacrificing themselves by having sex - for the good of all - with women.

Another cultural practice which may actually be related to culturally enforced of male-male competition is circumcision, which may reduce younger men's potential to illicitly father a child with an older man's wife. Some forms handicap sperm delivery in an obvious way; sub-incision is where cuts are made in the base of the penis causing sperm to be ejaculated from the base rather than the end (it is performed in several Aboriginal Australian societies). In some African and Micronesian cultures youths have one of their testicles crushed. One suggestion is that lack of a foreskin could make insertion or ejaculation slower, meaning brief, illicit sex is less likely to result in pregnancy. Illicit sex is proposed to be a worry of polygynous males. An anthropological database revealed that predictions of male circumcision tending to be a practice of non-monogamous societies was borne out - 48% of highly polygynous societies practice some form of male genital mutilation, and in societies in which wives live in separate households that increases to 63% while only 14% of the monogamous societies in the database practised genital mutilation of young men.

Geoffrey Miller, drawing on some of Darwin's largely neglected ideas about human behaviour, has hypothesized that human culture arose through a process of sexual selection. He argues that cultural traits such as art, music, dance, verbal creativity and humour are of no survival value. Miller is critical of theories that imply that human culture arose as accidents or by-products of human evolution. He believes that human culture arose through sexual selection for creative traits. In that view, many human artefacts could be considered subject to sexual selection as part of the extended phenotype, for instance clothing that enhance sexually selected traits. During human evolution, on at least two occasions, hominid brain size increased rapidly over a short period of time followed by a period of stasis. The first period of brain expansion occurred 2.5 million years ago, when *Homo habilis* first began using stone tools. The second period occurred 500,000 years ago, with the emergence of archaic *Homo sapiens*. Miller argues that the rapid increases in brain size would have occurred by a positive feedback loop resulting in runaway selection for larger brains. Tor Nørretranders, in *The Generous Man* conjectures how intelligence, musicality, artistic and social skills, language might have evolved as an example of the handicap principle, analogously with the peacock's tail, the standard example of that principle. Another hypothesis proposes that human intelligence is a courtship indicator of health and resistance against parasites and pathogens which are deleterious to human cognitive capabilities.

Human sexual anatomy

The theory of sexual selection has been used to explain a number of human anatomical features. These include rounded breasts, facial hair, pubic hair and penis size. The breasts of primates are flat, yet are able to produce sufficient milk for feeding their young. The breasts of non-lactating human females are filled with fatty tissue and not milk. Thus it has been suggested the rounded female breasts are signals of fertility. The evolutionary biologist Richard Dawkins has speculated that the loss of the penis bone in humans, when it is present in other primates, may be due to sexual selection by females looking for an honest advertisement of good health in prospective mates. Since a human erection relies on a hydraulic pumping system, erection failure is a sensitive early warning of certain kinds of physical and mental ill health. Homo also has by far the largest penis of the great apes and this may be sexually selected in much the same way as the larger testicles of Pan, another possibility is that the size of the human penis has resulted from selection for efficiency in displacing the sperm of rival males during intercourse.

Implications of differences in penis length and morphology

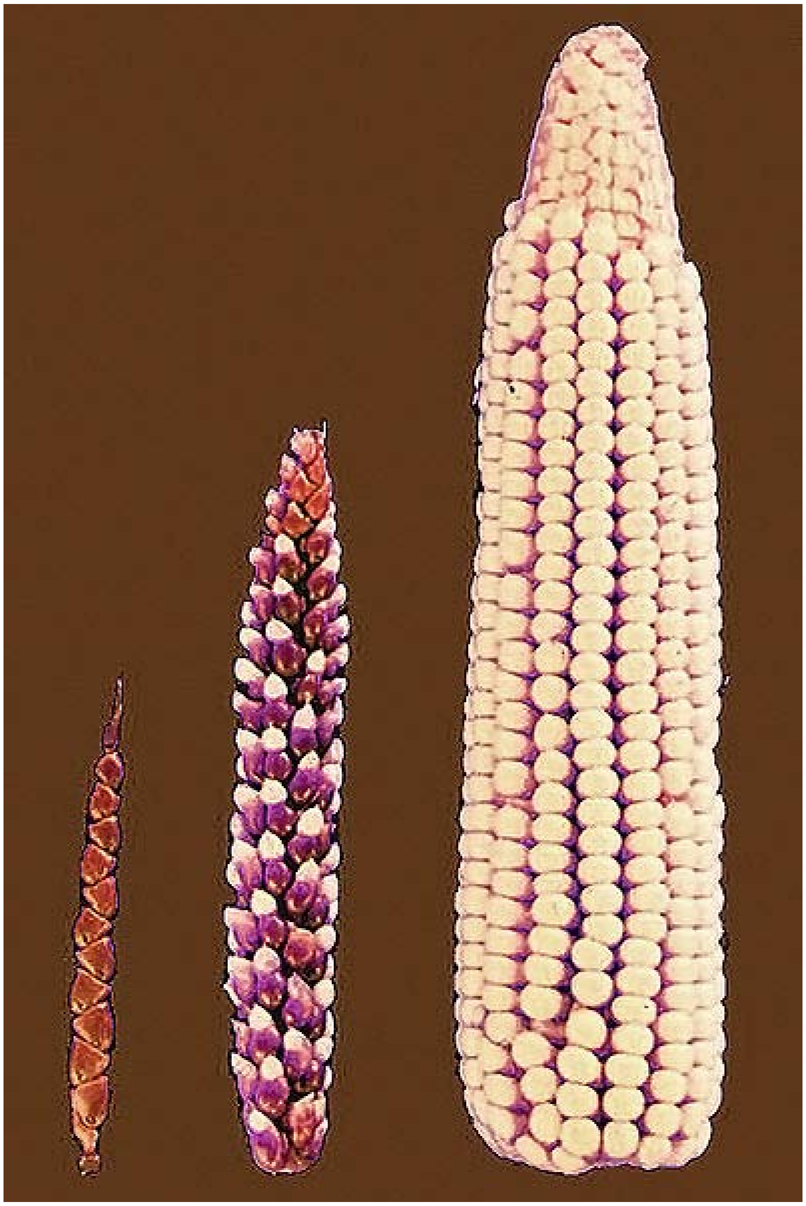
It has been suggested the evolution of the human penis towards larger size was the result of female choice rather than sperm competition because sperm competition generally favors large testicles and a small penis as in the chimpanzee. However the human penis has a larger glans ridge than is found in many other primates and this may function to displace other males' seminal fluid from a vagina by forcing it behind the glans during the thrusting of intercourse and hence expelling rival semen away from the area of the cervix. A model study showed displacement of semen was directly proportional to the depth of thrusting as an efficient semen displacement device. This study was simulating a situation where a woman had previously copulated with at least one man within a short period and found that a longer and thicker penis would more efficiently displace the semen of rival males by filling the vagina and forcing foreign semen out.

Chapter- 8

Theories and Concepts of Selection

Artificial selection

This Chihuahua mix and Great Dane show the wide range of dog breed sizes created using artificial selection.



Selective breeding transformed teosinte's few fruitcases (left) into modern corn's rows of exposed kernels (right).

Artificial selection (or selective breeding) describes intentional breeding for certain traits, or combination of traits. The term was utilized by Charles Darwin in contrast to natural selection, in which the differential reproduction of organisms with certain traits is attributed to improved survival or reproductive ability (“Darwinian fitness”). As opposed to artificial selection, in which humans favor specific traits, in natural selection the environment acts as a sieve through which only certain variations can pass.

The deliberate exploitation of artificial selection has become very common in experimental biology, as well as the discovery and invention of new drugs.

Artificial selection can also be unintentional; it is thought that domestication of crops by early humans was largely unintentional.

Historical development

Artificial selection was practiced by the Romans. Treatises as much as 2,000 years old give advice on selecting animals for different purposes, and these ancient works cite still older authorities, such as Mago the Carthaginian. The notion of artificial selection was later expressed by the Persian polymath Abu Rayhan Biruni in the 11th century. He noted the idea in his book entitled *India*, and gave various examples.

The agriculturist selects his corn, letting grow as much as he requires, and tearing out the remainder. The forester leaves those branches which he perceives to be excellent, whilst he cuts away all others. The bees kill those of their kind who only eat, but do not work in their beehive.

Charles Darwin coined the term as an illustration of his proposed wider process of natural selection. Darwin noted that many domesticated animals and plants had special properties that were developed by intentional animal and plant breeding from individuals that showed desirable characteristics, and discouraging the breeding of individuals with less desirable characteristics.

Darwin used the term twice in the 1859 first edition of his work *On the Origin of Species*, in Chapter IV: Natural Selection, and in Chapter VI: Difficulties on Theory –

Slow though the process of selection may be, if feeble man can do much by his powers of artificial selection, I can see no limit to the amount of change, to the beauty and infinite complexity of the coadaptations between all organic beings, one with another and with their physical conditions of life, which may be effected in the long course of time by nature's power of selection.

We are profoundly ignorant of the causes producing slight and unimportant variations; and we are immediately made conscious of this by reflecting on the differences in the breeds of our domesticated animals in different countries,—more especially in the less civilized countries where there has been but little artificial selection.

Contrast to natural selection

It should be emphasized that there is no real difference in the genetic processes underlying artificial and natural selection, and that the concept of artificial selection was used by Charles Darwin as an illustration of the wider process of natural selection. The selection process is termed "artificial" when human preferences or influences have a significant effect on the evolution of a particular population or species. Indeed, many evolutionary biologists view domestication as a type of natural selection and adaptive change that occurs as organisms are brought under the control of human beings.

However, it is useful to distinguish between artificial selection that is unintentional (or is intentional, but involves manipulating an organism's external environment only), and artificial selection that involves changing the organism's (internal) DNA sequence through modern laboratory techniques. In the latter case, the genetic process would have no counterpart to processes that occur in nature, and thus may be an exception to the point made in the previous paragraph concerning the lack of differences between the genetic processes underlying natural and artificial selection.

Laboratory usage

The deliberate exploitation of selective power has become common in experimental biology, particularly in microbiology and genetics. In a ubiquitous laboratory technique in genetic engineering, genes are introduced into cells in cell culture, usually bacteria, on a small circular DNA molecule called a plasmid in a process called transfection. The gene of interest is accompanied on the plasmid by a reporter gene, or "selectable marker", which encodes a specific trait such as antibiotic resistance or ability to grow in high salt concentrations. The cells can then be cultured in an environment that would kill normal cells, but is hospitable to those that have taken up and expressed the genes on the plasmid. In this way expression of the reporter gene serves as a signal that the gene of interest is also being expressed in the cells.

Another technique used in drug development uses an iterative selective process called *in vitro* selection to evolve aptamers, or nucleic acid fragments capable of binding specific organic compounds with high binding affinity.

Studies in evolutionary physiology, behavioral genetics, and other areas of organismal biology have also made use of deliberate artificial selection, though longer generation times and greater difficulty in breeding can make such projects challenging in vertebrates.

Negative selection (artificial selection)

In artificial selection, **negative selection** is where negative, rather than positive, traits of a species are selected for evolutionary continuance. It is generally not desirable, but may be caused by man-made conditions such as bad management, or like when humans eat the best plants or animals they have, leading to worse and worse stock; for example, it occurred frequently in primitive beekeeping. Another more recent example are regulations on fish and deer, where fish below a certain desired size will be set free, and deer suffering small antlers would less likely to be hunted, leading to undersized fish and small-antlered deer populations; the same case applies to the elephant's tusks.

Some proponents of Social Darwinism and eugenics argue that medicine and other technological, societal, and cultural practices cause negative selection in humans, better known as dysgenics. According to them, human manifests more and more negative traits.

In the case of microbiology and molecular biology, negative selection is used to screen for microorganisms that fail to possess a certain phenotype. An example of this is through replica plating.

Examples

The shellfishes *Concholepas concholepas* (Chilean abalone) and *Loxechinus albus* (Chilean sea urchin) have been exposed to over-extraction during a long time. Populations have shrunk and a recent study shows that extraction is making an artificial selection to eliminate faster-growing individuals. The same study also showed that populations in Chile are relatively homogeneous with low genetic variability.

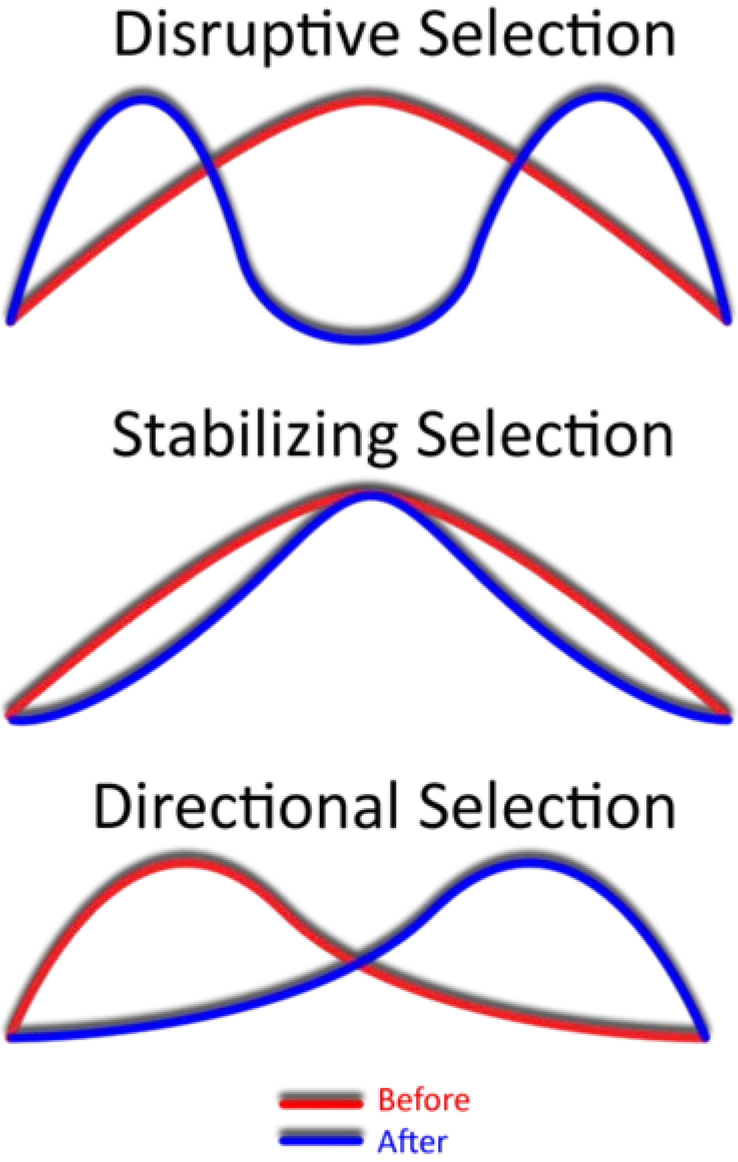
Negative selection (natural selection)

In natural selection, **negative selection** or **purifying selection** is the selective removal of alleles that are deleterious. This can result in stabilizing selection through the purging of deleterious variations that arise.

Purging of deleterious alleles can be achieved on the population genetics level, with as little as a single point mutation being the unit of selection. In such a case, individuals bearing the allele selected against might simply have less offspring on average generation after generation.

In the case of strong negative selection on a locus, the purging of deleterious variants will result in the occasional removal of linked variation, producing a decrease in the level of variation surrounding the locus under selection. The accidental purging of non-deleterious alleles due to such spatial proximity to deleterious alleles is called **background selection**. This effect increases with higher mutation rate but decreases with higher recombination rate.

Disruptive selection



A chart showing three types of selection

Disruptive selection, also called **diversifying selection**, describes changes in population genetics in which extreme values for a trait are favored over intermediate values. In this case, the variance of the trait increases and the population is divided into two distinct groups. This evolutionary process is believed to be the driving force behind sympatric speciation.

Example

Suppose there is a population of rabbits. The color of the rabbits is governed by two incompletely dominant traits: black fur represented by “B” and white fur represented by “b”. A rabbit with the genotype of “BB” would have a phenotype of black fur, a genotype of “Bb” would have gray fur (a display of both black and white) and a genotype of “bb” would have a phenotype of white fur.

If this population of rabbits were put into an area that had very dark black rocks as well as very white colored stone, the rabbits with black fur would be able to hide from predators amongst the black rocks and the white furred rabbits would be able to hide in the white rocks, but the gray furred rabbits would stand out in both of the habitats and would suffer greater predation.

As a consequence of the selective pressures of their environment, our hypothetical rabbit population would be disruptively selected for extreme values of the fur color trait: white or black, but not gray.

Significance

Disruptive selection is of particular significance in the history of evolutionary study, as it is involved in one of evolution's "cardinal cases", namely the finch populations observed by Darwin in the Galápagos.

He observed that the species of finches were similar enough to ostensibly have been descended from a single species. However, they exhibited disruptive variation in beak size. This variation appeared to be adaptively related to the seed size available on the respective islands (big beaks for big seeds, small beaks for small seeds). Medium beaks had difficulty retrieving small seeds and were also not tough enough for the bigger seeds, and were hence maladaptive.

While it is true that disruptive selection can lead to speciation, this is not as quick or straightforward of a process as other types of speciation or evolutionary change. This is largely because the results of disruptive selection are less stable than the results of directional selection (directional selection favours individuals at only one end of the spectrum).

For example, let us take the mathematically straightforward yet biologically improbable case of the rabbits: Suppose directional selection were taking place. The field only has dark rocks in it, so the darker the rabbit, the better. Eventually there will be a lot of black rabbits in the population (hence lots of “B” alleles) and a lesser amount of gray rabbits (who contribute 50% chromosomes with “B” allele and 50% chromosomes with “b” allele to the population). There will be few white rabbits (not very many contributors of chromosomes with “b” allele to the population). This could eventually lead to a situation in which chromosomes with “b” allele die out, making black the only possible colour for all subsequent rabbits. The reason for this is that there is nothing "boosting" the level of “b” chromosomes in the population. They can only go down, and eventually die out.

Consider now the case of disruptive selection. The result is equal numbers of black and white rabbits, and hence equal numbers of chromosomes with “B” or “b” allele, still floating around in that population. Every time a white rabbit mates with a black one, only gray rabbits results. So, in order for the results to "click", there needs to be a force causing white rabbits to choose other white rabbits, and black rabbits to choose other black ones. In the case of the finches, this "force" was geographic/niche isolation.

Ecological selection

Ecological selection (or **environmental selection** or **survival selection** or **individual selection** or **asexual selection**) refers to natural selection minus sexual selection, i.e. strictly ecological processes that operate on a species' inherited traits without reference to mating or secondary sex characteristics. The variant names describe varying circumstances where sexual selection is wholly suppressed as a mating factor.

Circumstances in which it occurs

Ecological selection can be said to be taking place in any circumstance where inheritance of specific traits is determined by ecology alone without direct sexual competition, when e.g. sexual competition is strictly ecological or economic, there is little or no mate choice, females do not resist any male who wishes to mate, all traits will be equally propagated regardless of mating, or the species is hermaphroditic or asexually reproducing, an ecological selection is taking place.

In sexually reproducing species, it is applicable mostly to situations where ecological pressures prevent most competitors from reaching maturity, or where crowding or pair-bonding or an extreme suppression of sexual selection factors prevents the normal sexual competition rituals and selection from taking place, but which also prevent artificial selection from operating, e.g. arranged marriages, where parents rather than the young select the mate based on economic or even astrological factors, and where the sexual desires of the mated pair are often subordinated to these factors, are artificial unless *wholly* based on an ecological factor such as control of land which is held by their own force.

Ecological selection vs sexual selection

In cases where ecological and sexual selection factors are strongly at odds, simultaneously encouraging and discouraging the same traits, it may also be important to distinguish them as sub-processes within natural selection.

For instance, *Ceratogaulus*, the Oligocene horned gopher, left in the fossil record a series of individuals with successively longer and longer horns, that seemed to be unrelated or maladaptive to its ecological niche. Some modern scientists have theorized that the horns were useful or impressive in mating rituals among males (although other scientists dispute this theory, pointing out that the horns were not sexually dimorphic) and that it was an example of runaway evolution. The species seems to have suddenly died out when horns reached approximately the body length of the animal itself, possibly because it could no longer run or evade predators - thus ecological selection seems to have ultimately trumped sexual.

It is also important to distinguish ecological selection in cases of extreme ecological abundance, e.g. the human built environment, cities or zoos, where sexual selection must generally predominate, as there is no threat of the species or individuals losing their ecological niche. Even in these situations, however, where survival is not in question, the variety and the quality of food, e.g. as presented by male to female monkeys in exchange for sex in some species, still has an impact on reproduction, however it becomes a sexual selection factor. Similar phenomena can be said to exist in humans e.g. the "mail order bride" who primarily mates for economic advantage.

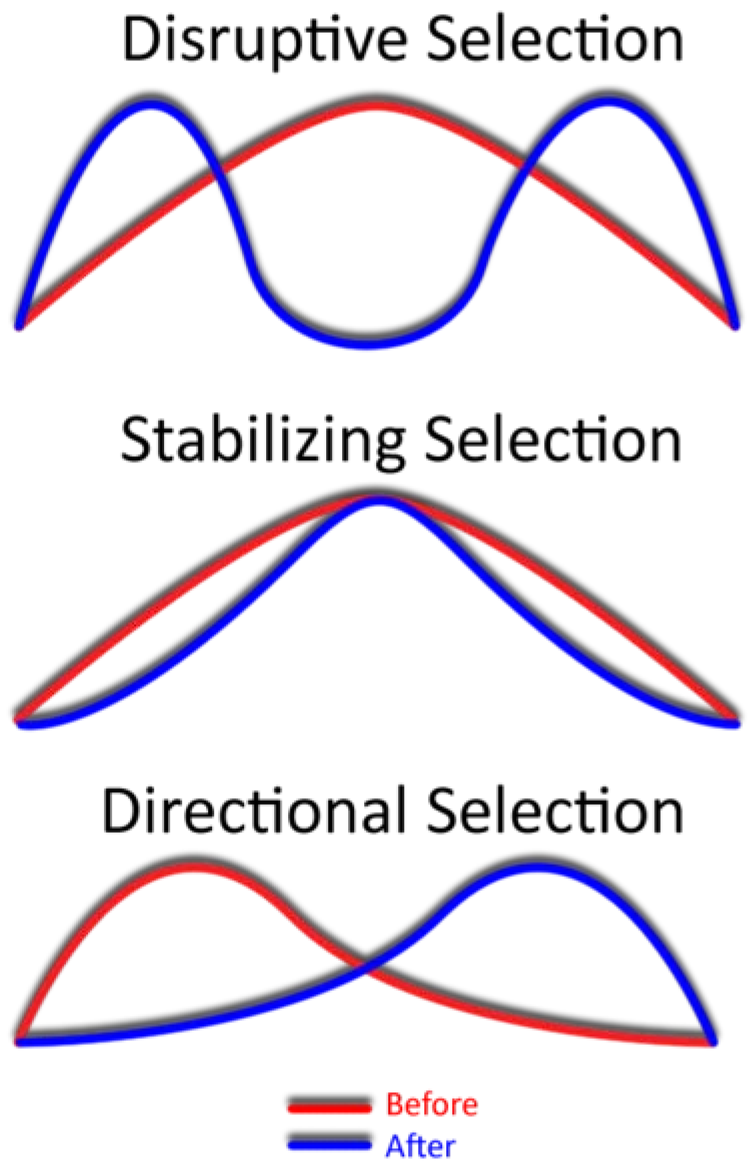
Differentiating ecological selection from sexual is useful especially in such extreme cases; Above examples demonstrate exceptions rather than a typical selection in the wild. In general, ecological selection is assumed to be the dominant process in natural selection, except in highly cognitive species that do not, or do not always, pair bond, e.g. walrus, gorilla, human. But even in these species, one would distinguish cases where isolated populations had no real choice of mates, or where the vast majority of individuals died before sexual maturity, leaving only the ecologically selected survivor to mate - regardless of its sexual fitness under normal sexual selection processes for that species.

For example, if only a few closely related males survive a natural disaster, and all are able to mate very widely due to lack of males, sexual selection has been suppressed by an ecological selection (the disaster). Such situations are usually temporary, characteristic of populations under extreme stress, for relatively short terms. However, they can drastically affect populations in that short time, sometimes eliminating all individuals susceptible to a pathogen, and thereby rendering all survivors immune. A few such catastrophic events where ecological selection predominates can lead to a population with specific advantages, e.g. in colonization when invading populations from more crowded disease-prone conditions arrive with antibodies to diseases, and the diseases themselves, which proceed to wipe out natives, clearing the way for the colonists.

In humans, the intervention of artificial devices such as ships or blankets may be enough to make some consider this an example of artificial selection. However it is clearly observed in other species, it seems unreasonable to differentiate colonization by ship from colonization by walking, and even the word "colony" is not specific to humans but refers generically to an intrusion of one species on an ecology to which it has not wholly adapted. So, despite the potential controversy, it may be better to consider all examples of colonist-borne diseases to be ecological selection.

For another example, in a region devastated by nuclear radiation, such as the Bikini Atoll, capacity to survive gamma rays to sexual maturity and (for the female) to term is a key ecological selection factor, although it is neither "natural" nor sexual. Some would call this too artificial selection, not natural or ecological, as the radiation does not enter the ecology as a factor save due to man's effort. Ambiguous artificial-plus-ecological factors may reasonably be called "environmental", and the term **environmental selection** may be preferable in these cases.

Directional selection



A chart showing three types of selection

Directional selection is a particular mode or mechanism of natural selection. In population genetics, **directional selection** occurs when natural selection favors a single phenotype and therefore allele frequency continuously shifts in one direction. Under directional selection, the advantageous allele will increase in frequency independently of its dominance relative to other alleles (i.e. even if the advantageous allele is recessive, it will eventually become fixed). Directional selection stands in contrast to balancing selection where selection may favor multiple alleles, and is the same as purifying selection which removes deleterious mutations from a population.

Apostatic selection

Apostatic selection is frequency-dependent selection by predators, particularly in regard to prey that are different morphs of a polymorphic species that is not a mimic (non-mimetic) of another species. It is closely linked to the idea of prey switching, however the two terms are regularly used to describe different aspects of the same phenomenon. Apostatic selection has been used by authors looking at the differences between different genetic morphs. In comparison, prey switching has been used when describing the choice between different species.

The idea links up with the concept of "search image" from Luuk Tinbergen, whereby - through experience - a predator is considered to have developed a particular skill or capacity to spot prey items of typical appearance (mainly pattern), to the point where typical specimens are even taken disproportionately to their actual abundance within the population. Conversely, specimens of unusual appearance are less likely to end up as part of a predator's diet than would be "justified" if consumption of food items was related to their abundance within the population in a straightforward way. In consequence, there are greater-than-"expected" chances of individuals within a population that are of non-typical appearance passing on the genes controlling that appearance to the next generation.

Chapter- 9

Unit of selection

A **unit of selection** is a biological entity within the hierarchy of biological organisation (e.g. genes, cells, individuals, groups, species) that is subject to natural selection. For several decades there has been intense debate among evolutionary biologists about the extent to which evolution has been shaped by selective pressures acting at these different levels.

This debate has been as much about what it means to be a unit of selection as it has about the relative importance of the units themselves, e.g., is it group or individual selection that has driven the evolution of altruism? When it is noted that altruism reduces the fitness of *individuals*, gene- or individual-centered explanations for the evolution of altruism become more complex and rely on the use of game theory, for instance; Kin selection.

Examples of selection at each level

Below, cases of selection at the genic, cellular, individual and group level from within the multi-level selection perspective are presented and discussed.

Selection at the level of the gene

George C. Williams in his influential book *Adaptation and Natural Selection* was one of the first to present a gene-centered view of evolution with the gene as the unit of selection, arguing that a unit of selection should exhibit a high degree of permanence.

Richard Dawkins has written several books popularizing and expanding the idea. According to Dawkins, genes cause phenotypes and a gene is 'judged' by its phenotypic effects. Dawkins distinguishes entities which survive or fail to survive ("replicators") from entities with temporary existence that interact directly with the environment ("vehicles"). Genes are "replicators" whereas individuals and groups of individuals are "vehicles". Dawkins argues that, although they are both aspects of the same process, "replicators" rather than "vehicles" should be preferred as units of selection. This is because replicators, owing to their permanence, should be regarded as the ultimate beneficiaries of adaptations. Genes are replicators and therefore the gene is the unit of selection. Dawkins further expounded this view in an entire chapter called 'God's utility function' in the book *River Out of Eden* where he explained that only genes alone have utility functions.

Some clear-cut examples of selection at the level of the gene include meiotic drive and retrotransposons. In both of these cases, gene sequences increase their relative frequency in a population without necessarily providing benefits at other levels of organization. Meiotic-drive mutations manipulate the machinery of chromosomal segregation so that chromosomes carrying the mutation are later found in more than half of the gametes produced by individuals heterozygous for the mutation, and for this reason the frequency of the mutation increases in the population.

Retrotransposons are DNA sequences that generate copies of themselves that later insert themselves in the genome more or less randomly. Such insertions can be very mutagenic and thus reduce drastically individual fitness, so that there is strong selection against elements that are very active. Meiotic-drive alleles have also been shown strongly to reduce individual fitness, clearly exemplifying the potential conflict between selection at different levels.

Selection at the level of the cell

Leo Buss in his book *The Evolution of Individuality* proposes that much of the evolution of development in metazoans reflects the conflict between selective pressures acting at the level of the cell and those acting at the level of the multicellular individual. This perspective can shed new light on phenomena as diverse as cancer, gastrulation, and germ line sequestration. Cancer, e.g., occurs when individual cells in the body mutate and develop the ability to proliferate without the restraints normally in place that serve the interests of the individual organism.

This selection for unconstrained proliferation is in conflict with the fitness interests of the individual, and thus there is tension between selection at the level of the cell and selection at the level of the individual. Since the proliferation of specific cells of the vertebrate immune system to fight off infecting pathogens is a case of programmed and exquisitely contained cellular proliferation, it represents a case of the individual manipulating selection at the level of the cell to enhance its own fitness. In the case of the vertebrate immune system, selection at the level of the cell and individual are not in conflict.

Selection at the level of individual organism

Selection at the level of the organism can be described as Darwinism, and is well understood and considered common. If a relatively faster gazelle manages to survive and reproduce more, the causation of the higher fitness of this gazelle can be fully accounted for if one looks at how individual gazelles fare under predation.

The speed of the faster gazelle could be caused by a single gene, be polygenic, or be fully environmentally determined, but the unit of selection in this case is the individual since speed is a property of each individual gazelle. In *The Selfish Gene*, Dawkins refers to this as a 'survival machine'.

Selection at the level of the group

If a group of organisms, owing to their interactions or division of labor, provides superior fitness compared to other groups, where the fitness of the group is higher or lower than the mean fitness of the constituent individuals, group selection can be declared to occur..

Specific syndromes of selective factors can create situations in which groups are selected because they display group properties which are selected-for. Many common examples of group traits are reducible to individual traits, however. Selection of these traits is thus more simply explained as selection of individual traits.

"Some mosquito-transmitted rabbit viruses are only transmitted to uninfected rabbits from infected rabbits which are still alive. This creates a selective pressure on every group of viruses already infecting a rabbit not to become too virulent and kill their host rabbit before enough mosquitoes have bitten it, since otherwise all the viruses inside the dead rabbit would rot with it. And indeed in natural systems such viruses display much lower virulence levels than do mutants of the same viruses that in laboratory culture readily outcompete non-virulent variants (or than do tick-transmitted viruses since ticks do bite dead rabbits)."

In the previous passage, the group is assumed to have "lower virulence", i.e., "virulence" is presented as a group trait. One could argue then that the selection is in fact against individual viruses that are too virulent. In this case, however, the fitness of all viruses within a rabbit is affected by what the group does to the rabbit. Indeed the proper, directly selected group property is that of "not killing the rabbit too early" rather than individual virulence. In situations such as these, we would expect there to be selection for cooperation amongst the viruses in a group in such a way that the group will not "kill the rabbit too early". It is of course true that any group behavior is the result of individual traits, such as individual viruses suppressing the virulence of their neighbours, but the causes of phenotypes are rarely the causes of fitness differences.

Species selection and selection at higher taxonomic levels

It remains controversial among biologists whether selection can operate at and above the level of species. One particular defender of the idea of species selection was Stephen Jay Gould who proposed the view that there exist macroevolutionary processes which shape evolution that are not driven by the microevolutionary mechanisms that are the basis of the Modern Synthesis. If one views species as entities that replicate (speciate) and die (go extinct), then species could be subject to selection and thus could change their occurrence over geological time, much as heritable selected-for traits change theirs over generations.

For evolution to be driven by species selection, differential success must be the result of selection upon species-intrinsic properties, rather than for properties of genes, cells, individuals, or populations within species. Such properties include, for example, population structure, their propensity to speciate, extinction rates, and geological persistence. While the fossil record shows differential persistence of species, examples of species-intrinsic properties subject to natural selection have been much harder to document.