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<u>Group Selection</u>
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<u>What is group selection?</u>
Group selection is the process by which variable groups, in a population of groups, compete and are differentially represented future generations. Heritable traits that increase the survival and reproductive success of groups will increase in frequency in the population of groups. Like any type of selection (natural, artificial, sexual, or otherwise) we need three components for selection to operate: heritability, variation, and differential survival or reproductive success.

Heritability requires a system of information transmission; early theories of group-selection, such as that of V. C. Wynn-Edwards (1986), assumed genetic inheritance. Traits that increase group fitness are transmitted to new group members via genetic reproduction of members. Many of the social insects transmit group-beneficial traits genetically. Argentine ants, a species that forms massive super-colonies, are currently invading North America, Asia, and Europe due to heritable willingness to cooperate with super-colony co-members and fight foreign super-colonies and the colonies of other species of ants (Pedersen et al. 2006). In this case, traits for out-group aggression and in-group cooperation are increasing in frequency as the Argentine super-colonies outcompete rivals in both survival and reproductive success.

Greater amounts of variation between groups leads to a greater potential for group selection. When no or very small amounts of variation exist, selection pressures are absent or extremely weak. When statistically distinct groups exist (these do not have to be geographically determined), we observe selective forces at work when there is a struggle for existence between groups. Genetic kin share genes and create an opportunity for small-scale group selection (Hamilton, 1964). Three mechanisms can increase the size of groups subject to kin selection: high rates of inbreeding, clonal reproduction, and high fecundity, as in social insect queens. Most mammalian species, being rather outbred, obligate sexual reproducers with modest fecundity very rarely generate large complex societies by the kin selection route. Many evolutionary biologists today think that most group-beneficial traits, such as cooperative behavior, are due to kin selection because descent from a close common ancestor is the most common way that significant genetic variation between groups can arise in nature.

Humans are a conspicuous exception; in tribes, much less in nation-states, humans cooperate with quite distantly related people to compete with other tribes or nations that typically differ little genetically from themselves. To explain this pattern, some investigators have proposed that selection may be acting on cultural differences between groups rather than genetic ones (Bell et al. 2009).

Groups replicate themselves via social learning among members and cultural groups are often distinct entities within a population of competing cultural groups. Culturally, group selection applies to the increase in frequency of traits in the larger population that contribute to the comparative success of a cultural group against other groups. One example of a behavior that contributes to the good of the group is altruism (helping others at a cost to oneself). For example, those who risk their lives to fight for a tribe contribute to the survival of the tribe and to its reproduction if it can expand into the territory of a defeated tribe. Examples of differential success of culture groups include competition between religions for converts, competition between firms to succeed in the marketplace, and competition between factions to control the distribution of political spoils. Currently, two factors contribute to the disagreements surrounding group selection: 1) Confusion of genetic and cultural group selection, and 2) Improper consideration of multiple levels of selection acting on individuals.

Modeling group selection
Evolutionists often partition an organism's fitness into components that generate fitness tradeoffs. Sexual selection can produce traits that increase reproductive success at the cost of survival. Kin selection can produce traits that increase the fitness of close relatives at a cost to individual fitness. Group selection is another extension of this partitioning. When individuals live in groups, individual survival and reproductive success may be affected by the survival and reproductive success of their group. At the same time selfish individuals who don't make costly contributions to group success but benefit from it anyway, will be favored within groups. Selection at two levels of organization sets up a potentially stark tradeoff depending on the degree to which individuals share the same heritable variant. If group members share no heritable variation, the conflict will be quite stark. If they have the same heritable variant their evolutionary interest will be perfectly aligned. If they share their cultural variants but not their genetic variants a tradeoff arises between genetic and cultural fitness.

The Selfish Gene and multi-level selection
The gene's-eye view of the world has become a way to popularize the theory of natural selection to non-specialists (Dawkins 1976). Genes that increase the survival and reproductive success of their carriers should increase in a population over time. These genes are "selfish" in the sense that we expect them to produce behavior that will make their carriers increase the frequency of themselves. Since close relatives often carry the same genetic material, researchers use this idea to explain the altruistic behavior between kin that we observe in many species. Altruistic behavior was once a paradox from an evolutionary perspective - individuals that decrease their own fitness in order to increase that of another should have been selected out of past populations.

The concept of the "selfish-gene" must be understood to include the sum total of a gene's likelihood of being represented in future generations via direct fitness (that of the individual) and indirect fitness (that of the individuals relatives who also carry the gene). This total is referred to as inclusive fitness, and it helps to understand how a gene may flourish in a population when relatives survive to reproduce, even though it may decrease the fitness of a particular individual.

Other mechanisms that increase genes for altruism also rely on ensuring that altruistic individuals are able to recoup their immediate losses in the future (reciprocal altruism). It should be noted that these are decision-making mechanisms. The likelihood of altruistic behavior is tempered by the likelihood of recouping losses - the average relatedness between individuals or the probability of future interactions. And yet much of human behavior remains unexplained from this gene's-eye view. We perform altruistic acts in large groups of non-kin, often anonymously. Deductively we are left with an explanation involving trade-offs between different components of fitness. One method is to partition components into different levels (Keller, 1999).

In 1972, George R. Price published a general equation of natural selection that predicts whether an allele will increase in frequency depending on the different types of natural selection that affect the trait. From his perspective, it did not make sense to consider only one special case of natural selection at a time, but add up the positive and negative forces on traits. This is referred to as multi-level selection.

Even the selfish-gene is dependent on the concept of multi-level selection, balancing direct and indirect fitness. The accepted unit of selection, phenotype, only exists at the level of an organism - and what is an organism but a group of genes? So we have multiple levels of selection simultaneously occurring. The allele's own effect on phenotype, and the concerted effort of all the alleles in an organism creates a complex whole. A gene succeeds when its organism succeeds. An organism may likewise succeed when its group succeeds.

Sometimes a particular level of selection may have little or no effect on an organism's fitness. Many animal species do not live in groups, and have little to no effect of group success on the transmission of an individual's genetic material. For many other species, groups may exist socially, but genetic material is exchanged frequently enough that migration of genetic material quickly swamps any mutation that may maintain genetic variation between groups.

How cultural evolution generates heritable between group variation
Because cultural evolution can occur rapidly, compared to genetic evolution, cultural variation between groups may exist despite large amounts of migration between groups. Humans also often bias their social learning in favor members of their own social group and to preferentially adopt the behavior of those in the majority. Such tendencies protect variation between groups by discriminating against migrants from other groups. The same rate of migration that tends to make neighboring human groups almost identical genetically leaves them with different languages, different religions and different social institutions. Even different companies recruiting from the same population can instill different corporate cultures in trainee employees. Within the Roman Empire, norms for altruistic acts to in-group members of early Christians attracted converts and increased their survival during times of plague. In a few centuries, Christianity grew to be the dominant religion of Western Europe (Stark, 1997).

Gene-culture co-evolution
Multi-level selection potentially exerts different forces on genetic and cultural variation. This suggests that genes and culture will evolve to exert selective forces on each other. Lumsden and Wilson (1981) argued that "epigenetic rules" would evolve to make sure that cultural variation conformed to the needs of genetic fitness. Given the spectacular success of our species as a biological population epigenetic rules certainly seem to have been effective. But culture creates environments that often persist long enough to exert selection on genetic variants. A classic example is the development of lactose tolerance among adults. A long history of dairying led to an increase in alleles that confer the ability to digest milk sugars as adults, in not one, but four separate populations (Check 2006)!

This back-and-forth gene-culture coevolution leads to unexpected twists in human evolution. Richerson and Boyd (2001) argue that cultural evolution favored cooperation on a scale that selection on genes could never achieve on its own and that it accomplished this trick by taming selfish epigenetic rules. Culturally transmitted social institutions prescribe rewards for people who conform to society's social norms and punishment for those who disobey them. Any genetic variation in tendencies to conform to norms may thus fall under social selection. Human tendencies to punish norm violators, identify with their social groups, and cooperate readily with strangers who belong to the group may be genetic traits that were favored by culture based social selection once culture became an important human adaptation well back in the Pleistocene.

The controversy over cultural group selection
Stephen Pinker (2012) wrote a strong critique of the idea that culture can be subject to group selection, indeed that it can be conceived of as evolving in the same sense as genes at all. A considerable number of commentators on Pinker's essay supported his attack while others defended cultural evolution and cultural group selection.

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