

Group selection

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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 fitness of individuals within that group.

Group selection was used as a popular explanation for adaptations, especially by V.C. Wynne-Edwards. However, critiques, particularly by George C. Williams in his 1966 book *Adaptation and Natural Selection*, John Maynard Smith (1964) and C.M. Perrins (1964) cast serious doubt on group selection as a major mechanism of evolution, and led to a more gene-centric view of evolution.

Overview

Theoretical models of the 1960s seemed to imply that the effect of group selection was negligible. Genetic variation, the raw material of selection, is much higher between individuals than it is between groups, particularly as groups grow larger. Alleles are likely to be held on a population-wide level, leaving nothing for group selection to select for. In addition, most phenotypes, particularly physical ones, are not highly heritable in the first place. 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 theoretical models ever would have predicted (e.g., Wade 1977). 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., Goodnight and Stevens 1997). 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 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 (Rauch et al, 2003) and through social communication (Werfel & Bar-Yam, 2004), 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.

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 Elliot Sober and David Sloan Wilson 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, if groups can also be "vehicles" for selection. For example, groups that cooperate better may have out-reproduced those which did not. Resurrected in this way, Sober & Wilson's new group selection is usually called multilevel selection theory.

Although Richard Dawkins and fellow advocates of the gene-centered view of evolution remain unconvinced (see, for example, Cronk, 1994; Dawkins, 1994; Dennett, 1994), Sober and Wilson'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 (often regarded as the father of sociobiology) argued that kin selection could no longer be thought of as underlying the evolution of extreme sociality, for two reasons. First, Trivers and others have shown that the argument that haplodiploid inheritance, characteristic of the Hymenoptera, creates a strong selection pressure towards nonreproductive castes is mathematically flawed. Secondly, 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 replacing Hamilton's equation

$$rb > c$$

(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, even more recently, it has been argued that EO Wilson made a series of basic errors in logic in making these arguments and infact that kin selection and group selection are infact not in opposition at all (Foster et al. 2006). Indeed, this is the view taken by the vast majority of modern sociobiologists.

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