Group Selection ☆

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Glossary

Adaptation The appearance of design in the living world, originally attributed to deities and now known to be due to natural selection.
Between-group selection The part of natural selection that owes either to the impact of the group character upon individual fitness (contextual-analysis approach) or to the differential fitness of groups (levels-of-selection approach).
Contextual analysis An approach to group selection theory that defines group selection as that component of natural selection ascribable to the impact of the group character upon individual fitness.
Group adaptation The appearance of design at the group level, driven by between-group selection, that obtains only when within-group selection is negligible.
Inclusive fitness The quantity that individuals appear designed to maximize as a consequence of the action of natural selection.
Kin selection theory A theory of social evolution that partitions natural selection into its direct (impact of an individual's character on her own fitness) and indirect (impact of an individual's character on the fitness of her genetic relations) components.
Levels of selection An approach to group selection theory that defines group selection as that component of natural selection that owes to the differential fitness of groups.
Natural selection The component of evolutionary change in heritable characters that owes to fitness differences between individuals (within and between groups, and mediated by their own characters and those of their social groups).
Superorganism The idea that a social group can be considered an adapted organism in its own right, which is valid only in the absence of conflicts of interest within the group.
Within-group selection The part of natural selection that owes either to the impact of the individual's character upon her own fitness (contextual-analysis approach) or to the differential fitness of individuals within groups (levels-of-selection approach).

The Origin of Group Selection

As with many of the big ideas in evolutionary biology, the concept of group selection has its origins in the writings of Charles Darwin. Darwin discussed problems of social evolution in *The Origin of Species*, focusing upon the paradox presented by the sterile castes of social insect colonies. Here, the problem is to explain how the exquisite adaptations exhibited by these individuals (and, indeed, that are unique to them) could be molded by natural selection, given that these individuals do not produce offspring. His solution was to notice that kin tend to share heritable characters in common such that, for example, a cattle breeder who slaughters an animal and finds that it has particularly good meat can select for this character by preferentially breeding from the close relatives of the slaughtered individual. Hence, sterile workers can evolve adaptations, provided these improve the fitness of their fertile family members. This is the theory of kin selection, which was more fully elaborated a century later by W.D. Hamilton.

In the *Descent of Man*, Darwin took an alternative approach to understanding social traits. He noted that those human behaviors considered moral typically place the individual at a fitness disadvantage relative to her social partners, but benefit the social group as a whole. Darwin suggested that these behaviors could have been driven by natural selection acting at the group level. Groups of ancestral humans would have come into conflict over limiting resources, and Darwin suggested that the resulting selection for the most cooperative groups would often have overpowered the selection operating against such cooperation within groups. This was the launch of the theory of group selection, which for many years was considered empirically distinct from the kin selection hypothesis. Interestingly, Darwin himself did not clearly distinguish the two ideas, pointing to blood relationship between group mates as a key factor driving the individual's incentive to act for the good of her group.

The Modern Theory of Group Selection

Today, we – like Darwin – understand that the kin selection and group selection approaches to social evolution are exactly equivalent. Both describe the same evolutionary process, that is, natural selection, but split up its action in somewhat different ways. The kin selection approach splits natural selection into the direct effect of a heritable character on the individual's own reproductive success and the indirect effect of the character on the reproductive success of the individual's genetic relatives. The group selection approach instead splits natural selection into its within-group and between-group components. Irrespective of how

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one chooses to split up the components of natural selection, they will always add to give the same sum, and so kin selection and group selection theories yield exactly the same predictions about social evolution.

However, there is some disagreement as to exactly how the group selection split should be made. The first – and perhaps most popular – approach to the theory of group selection is that pioneered by George Price and subsequently developed by William Hamilton, which has been termed the "levels-of-selection" approach. This takes Price's general equation of natural selection as a starting point:

$$\Delta_{\mathrm{NS}}E(g) = \mathrm{cov}(v, g) \tag{1}$$

Price's equation expresses the change in the average value of any heritable character between consecutive generations, under the action of natural selection, as being equal to the covariance of relative fitness v and character value g over all the individuals in the population. Assigning individuals to groups (for simplicity, I assume that there is an equal number of individuals in every group), and assigning every group a unique index $i \in I$ and every individual within each group a unique index $i \in J$, Eq. (1) can be partitioned into the between-group and average within-group covariance between relative fitness and character value:

$$\Delta_{\mathrm{NS}}E(g) = \mathrm{cov}_I(v_i, g_i) + E_I(\mathrm{cov}_J(v_{ij}, g_{ij})) \tag{2}$$

where $v_i = E_J(v_{ij})$ and $g_i = E_J(g_{ij})$ are the average fitness and character value, respectively, among the individuals belonging to the ith group.

The first term on the right-hand side (RHS) of Eq. (2) is the covariance of group fitness and group character value, taken over all the groups in the population, and defines the action of "between-group" selection. The second term on the RHS of Eq. (2) is the average, taken over all groups in the population, of the covariance between individual fitness and individual character value, taken over all the individuals within each group, and defines the action of "within-group" selection. Between-group selection tends to be stronger when there is a larger variance in fitness between groups (eg, owing to large group benefits of the character) and when there is a larger variance in character value between groups (eg, owing to group mates being genetically similar blood relations). Within-group selection tends to be stronger when there is a larger variance in fitness within groups (eg, owing to large within-group costs of the character) and when there is a larger variance in character value within groups (eg, owing to group mates being genetically dissimilar nonrelatives).

One feature of the levels-of-selection approach, which has sometimes been considered undesirable of a theory of group selection, is its tendency to diagnose between-group selection even for characters that are not social. For example, if the character in question relates to liver function, and if some groups happen to contain more individuals with defective livers than do other groups, then a component of natural selection acting upon liver function would operate at the between-group level. To avoid this problem, a second approach to the theory of group selection has been devised that partitions Price's equation in a slightly different way. This is the contextual-analysis approach, introduced by Lorraine Heisler and John Damuth, and it splits up Eq. (1) as follows:

$$\Delta_{\mathrm{NS}}E(g) = \beta(v_{ij}, g_{ij}|g_i)\mathrm{cov}(g_{ij}, g_{ij}) + \beta(v_{ij}, g_i|g_{ij})\mathrm{cov}(g_i, g_{ij}) \tag{3}$$

where β terms are partial regression coefficients obtained by fitting the linear multiregression model $E(v_{ij}|g_{ij}$ and $g_i) = E(v_{ij}) + \beta(v_{ij}, g_{ij}|g_i)(g_{ij} - E(g_{ij})) + \beta(v_{ij}, g_i|g_{ij})(g_i - E(g_{ij})) + \epsilon_{ij}$ to the population (g_{ij}, g_i, v_{ij}) data by means of least squares (ie, minimizing the quantity $E(\varepsilon_{ij}^2)$). The $\beta(v_{ij}, g_{ij}|g_i)$ term describes the effect of the individual's character value on her own fitness, holding fixed any effect of her group's average character value, and so the quantity $\beta(v_{ij}, g_{ij}|g_{ij})\mathrm{cov}(g_i, g_{ij})$ has been interpreted as a form of within-group selection. Conversely, the $\beta(v_{ij}, g_i|g_{ij})$ term describes the effect of the group's average character value on the individual's fitness, holding fixed any effect of her own character value, and so the quantity $\beta(v_{ij}, g_i|g_{ij})\mathrm{cov}(g_i, g_{ij})$ has been interpreted as a form of between-group selection.

The contextual-analysis approach avoids diagnosing group selection for nonsocial traits. However, it does diagnose the action of group selection even in scenarios where there are no fitness differences between groups. For example, if density-dependent regulation maintains all groups at a fixed size, then individuals with defective livers may achieve high fitness, provided that their group mates also have defective livers, but will achieve lower fitness if their group mates primarily have properly functioning livers. Contextual analysis suggests that group selection is acting here and, moreover, that it favors defective livers, even though they bring no advantage to the group as a whole.

As a consequence of such perceived failures of levels-of-selection and contextual-analysis approaches to the theory of group selection, some authors – including David Wilson and Edward Wilson – have suggested that group selection defies formal analysis altogether. However, a more pragmatic outlook recognizes that the alternative approaches address somewhat different problems, and in a potentially useful way. Sometimes, it is helpful to know how the fitness–character covariance that defines natural selection and drives Darwinian adaptation is distributed within and between groups. And sometimes it is helpful to know how individual and group characters impact upon individual fitness. Hence, the levels-of-selection and contextual-analysis approaches may be more fruitfully regarded as complementary tools, each providing its own helpful insights, and not as competing theories of group selection.

Group Adaptation

The theory of group selection has suffered a turbulent history, with heated debate going well beyond the relatively minor disagreements as to whether a levels-of-selection or a contextual-analysis approach is more appropriate. Much of this turbulence arises out of a basic confusion of the ideas of selection and adaptation, with the respectable notion of selection operating at the level of the group being confused with the idea of the group as a superorganism that exhibits adaptations in its own right. Infamously, Vero Wynne-Edwards argued that between-group selection would necessarily trump within-group selection, leading to behavior that is optimized for the good of the group and not for the good of the individual. This group adaptationism is naive, and was rightly rejected by the leading sociobiologists of Wynne-Edwards' day. Natural selection leads to adaptation at the level of individual organisms: irrespective of the intensity of selection within and between groups, individuals are adapted to maximize their inclusive fitness. Only when within-group selection is abolished, by factors such as clonal relatedness or complete repression of competition between group mates, can social groups be considered adaptive units in their own right. Such occurrences of group-level adaptation are relatively rare, and are studied within the framework of the major transitions in evolution.

Summary and Conclusion

The theories of kin selection and group selection arose as alternative ways of understanding the evolution of social characters. Today, we understand that these theories are mathematically equivalent, and always lead to the same empirical predictions. Within the group selection literature, there remains disagreement as to how the notion of group selection is best formulated, with some researchers favoring a levels-of-selection approach and others favoring a contextual-analysis approach. It would be most fruitful to consider these not as competing hypotheses but rather as complementary approaches that address somewhat different issues in social evolution. Care must be taken so as not to confuse group selection with group adaptation: while the former is ubiquitous in the natural world, the latter obtains only in special circumstances where within-group conflict is effectively abolished, owing to clonal relatedness or repression of competition between the members of the group.

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