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# EIGHT CRITICISMS NOT TO MAKE ABOUT GROUP SELECTION

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**Group selection, which was once widely rejected as a significant evolutionary force, is now accepted by all who seriously study the subject. There is still widespread confusion about group selection, however, not only among students and the general public, but among professional evolutionists who do not directly study the subject. We list eight criticisms that are frequently invoked against group selection, which can be permanently laid to rest based upon current knowledge. Experts will always find something to critique about group selection, as for any important subject, but these eight criticisms are not among them. Laying them to rest will enable authors to openly use the term group selection without being handicapped during the review process.**

**KEY WORDS: Group selection, multilevel selection, peer review process.**

*"Please remove all references to group selection. . . significant or not, group selection is not going on here."*

"*It is all very well to look at success within and between groups, but can you really extrapolate this to group selection?"*

*"What the authors show is not group selection, but rather that . . . mating success depends on the social environment"*

*" This is a controversial topic, worthy of a mention, but not worthy of the extended discussion, because it is largely lacking in both formal theory and empirical support to justify it."*

"*I am not sure how this behavior can be maintained under a group selection scenario unless there is no dispersal and populations frequently go extinct."*

–anonymous reviews of manuscripts framed explicitly in terms of group selection

Group selection is the evolution of traits based on the differential survival and productivity of groups. It was first proposed by Darwin (1871), who observed that social adaptations frequently are not locally advantageous. The paradigmatic example is altruism, which is good for the group but vulnerable to more selfish behaviors within the group. How can a behavior evolve in the total population when it is selectively disadvantageous within each and every group? Only if it is selectively advantageous at a larger scale. Groups with more altruists robustly outcompete groups with more selfish individuals, which can counterbalance the selective disadvantage of altruism within groups. Sober (2011) has recently cataloged Darwin's thoughts on group selection in the entire corpus of his work.

Group selection appeared to be authoritatively rejected in the 1960s, as every student of evolutionary biology knows. The verdict was that group selection is theoretically possible but that in reality, selection within groups is almost invariably stronger than selection among groups. As George C. Williams (1966, p. 93) put it in *Adaptation and Natural Selection*, "group-related adaptations do not, in fact, exist." Following the rejection of group selection, what looked like altruism was explained in terms of individual or genetic self-interest, based on theoretical frameworks such as inclusive fitness theory, evolutionary game theory and selfish gene theory (reviewed by Sober and Wilson 1998).

All of these theoretical frameworks were regarded as alternatives to group selection until George Price convinced W.D. Hamilton that Darwin's explanation was embedded in inclusive

fitness theory. Hamilton's method of calculating the effect of an altruistic behavior on the absolute number of copies of the altruistic gene identical by descent in both the donor and recipient considered only net effects, summing the selective differentials within and between groups. Price's (1970, 1972) method explicitly partitioned selection into within and between group components. When Hamilton viewed his own theory through the lens of the Price equation, he saw that altruism is selectively disadvantageous within groups and evolves only by virtue of the differential contribution of groups to the total gene pool, exactly as Darwin envisioned. The importance of kinship was that it increased genetic variation among groups, thereby strengthening between-group selection compared to within-group selection. Hamiltonpublished his revised interpretation of inclusive fitness theory, clearly framed in terms of multilevel selection, in 1975. This fascinating period in the history of evolutionary thought has recently been recounted for a general audience by Harman (2010).

Since then, it has become clear that Hamilton's revised interpretation of inclusive fitness theory applies to all evolutionary theories of social behavior. All assume that social interactions take place in groups that are small compared to the total population, that traits termed "altruistic" and "cooperative" are selectively disadvantageous within groups, and require the differential contribution of groups to the total population to evolve. The reason that the logic of multilevel selection is not transparent is because selection differentials are typically calculated at the level of the total population, by averaging the fitness of individuals or genes across groups, without also calculating selection differentials within groups. What evolves in the total population is then labeled individually or genetically advantageous, as if group selection need not be invoked, when in fact group selection is the force that provides the selective advantage. It is impossible to evaluate whether a given trait evolves by group selection unless local and global selection differentials are compared to each other.

Based on these and other developments, group selection has made a transition from a process that should never be invoked to one that is indisputably a significant evolutionary force in nature. Even Andy Gardner, a critic of multilevel selection theory in some respects, acknowledged in a 2008 commentary published in *Nature* that "everyone agrees that group selection occurs" (Kohn 2008 p. 296). Unfortunately, "everyone" refers only to those who seriously study the subject. An enormous amount of confusion about group selection still exists among the general public, students learning from outdated textbooks, and professional evolutionists who are expert on other topics but have not kept up with the literature on multilevel selection.

Confusion at the professional level is reflected in the peer-review process. When a manuscript or grant proposal on a given topic is framed explicitly in terms of group selection, it is typically sent for review to experts on the topic regardless of their familiarity with group selection. Their comments frequently reveal outdated views about group selection, despite their qualifications for the topic at hand, as illustrated by the passages quoted at the beginning of this article. A typical recommendation is to publish the article but only after references to group selection have been removed. Other reviewers, who are knowledgeable about group selection in addition to the topic at hand, may well recommend that the article should be published as an outstanding example of group selection and the utility of an explicitly multilevel approach. At this point, authors who wish to retain an explicitly multilevel perspective must engage in a protracted struggle with the hostile reviewers, often with an uncertain editor acting as the referee.

In an attempt to remedy these misunderstandings, we list eight criticisms that are frequently invoked against group selection, which can be permanently laid to rest based upon current knowledge. Experts will always find something to critique about group selection, as for any important subject, but these criticisms are not among them.

***Criticism No. 1: The Fact That a Trait Evolves in the Total Population is an Argument Against Group Selection.*** Whenever a trait evolves by natural selection in the total population, it has a higher fitness than the trait that did not evolve, all things considered. This is a tautology and does not qualify as an argument against group selection. The distinction between individual and group selection requires a comparison of fitness differentials within and among groups in a multigroup population. When a trait evolves by group selection, despite being selectively disadvantageous within groups, it too is more fit than the trait did not evolve, all things considered. Simply put, the need to invoke group selection cannot be evaluated unless selection differentials at the local scale are compared with selection differentials in the total population.

Although within- and between-group selection frequently favor different traits, resulting in a conflict between levels of selection, they can also favor the same trait, in which case group selection accelerates the rate that the trait evolves. Statistical methods such as the Price equation (Price 1970, 1972) and contextual analysis (Heisler and Damuth 1987, Goodnight et al. 1992) enable overall selection in the total population to be partitioned into within- and between-group components regardless of whether they are opposed or in the same direction. However, these methods can also misclassify certain cases. For example, a trait that increases the fitness of individuals without any social effects will evolve regardless of how the individuals are distributed into groups, but can still be reflected in the group component of the Price equation depending upon how the individuals are grouped. Because multilevel selection is a causal process, no correlational method should be expected to correctly classify every case (for an extended discussion of

these more advanced issues see Okasha 2006). For the purposes of this commentary, the important point to stress is that what evolves in the total population is no argument at all against group selection.

***Criticism No. 2: If a Trait Increases the Absolute Fitness of an Individual, it Does Not Require Group Selection to Evolve.*** Maximizing one's absolute fitness is not the same as maximizing one's relative fitness within groups. Knowing the effect of a trait on the absolute fitness of the actor simply does not provide the information required to evaluate whether group selection needs to be invoked, as outlined in (1). One of the core messages of G.C. Williams' *Adaptation and Natural Selection* (1966) is that natural selection is based on relative fitness, making it curious that anyone would regard absolute individual fitness as sufficient information for deciding what might evolve by natural selection at any level.

***Criticism No. 3: Conceptualizing the Group as the Social Environment of the Individual is an Argument Against Group Selection.*** This is often a useful heuristic for thinking about what evolves in the total population, but it is a variant of (1) as far as evaluating group selection is concerned. Anyone who uses this heuristic can easily check to see if group selection needs to be invoked by comparing the relative fitness of alternative traits within groups.

***Criticism No. 4: Frequency-dependent Selection is an Argument Against Group Selection.*** Virtually all forms of group selection are frequency dependent because the fitness of an individual depends upon the phenotypes of others in its group in addition to its own phenotype. However, the mere fact of frequency dependence says nothing about whether group selection needs to be invoked, because frequency dependence can take place entirely within groups, in which case there is no group selection. The need to invoke group selection must be assessed on the basis of selection differentials within and among groups, not the raw fact of frequency dependence.

***Criticism No. 5: The Fact That a Trait Can Be Measured in Individuals Means That It Evolved by Individual-level Selection.*** In his excellent book on multilevel selection, Okasha (2006) distinguished between "type 1" and "type 2" group selection, depending upon whether the trait can be measured in individuals or is inherently the property of a group. This distinction is useful for some purposes but cannot be used as a criterion for deciding whether a trait evolves by group selection, as Okasha also stresses. Not only are the classic examples of group selection measurable at the individual level (e.g., altruism), but traits such as group size that cannot be measured in individuals can evolve entirely by within-group selection.

***Criticism No. 6: Group Selection is Theoretically Implausible.*** Group selection was rejected in the 1960s largely because it seemed theoretically implausible, not because of a great weight of empirical evidence. The models at the time indicated that between-group selection would usually be weak compared to within-group selection. No theoretical biologist knowledgeable about multilevel selection would support this statement today. In the first place, all evolutionary models of social behavior include the logic of multilevel selection, as shown by formalisms such as the Price equation (1970, 1972) and contextual analysis (Heisler and Damuth 1987, Goodnight et al. 1992). In the second place, even some of the classic group selection scenarios that were regarded as theoretically implausible, such as Wynne-Edwards' (1962, 1986) hypothesis that animal populations can evolve to avoid overexploiting their resources, have been shown to be theoretically plausible under biologically realistic conditions (e.g., Werfel and Bar-Yam 2004).

***Criticism No. 7: There is Little Empirical Support for Group Selection.*** The empirical case against group selection in the 1960s was argued largely on the basis of parsimony, with very few empirical examples in which selection within and among groups had been actually measured (see Sober and Wilson 1998, Sober 2011). Williams (1992) regarded sex ratio as the best documented example of a trait that evolves purely by within-group selection. Now it provides one of the best examples of multilevel selection, in which the sex ratio that evolves in the total population does not necessarily maximize relative fitness within single groups. A study of phage viruses feeding on *Escherichia coli* in multigroup laboratory populations provides strong empirical evidence for Wynne-Edwards' hypothesis (Kerr et al. 2006). If there were no empirical support for group selection, then the between-group terms of statistical partitioning methods such as the Price equation and contextual analysis would always be negligible compared to the within-group terms. No one familiar with the empirical literature would make this statement (e.g., Goodnight and Stevens 1997, Wilson and Wilson 2007).

***Criticism No. 8: Group Selection Requires Limited Dispersal Among Groups.*** Group selection was regarded as implausible in the 1960s based in part on the following theoretical argument: (1) group selection requires genetic variation among groups; (2) genetic variation is eroded by dispersal; (3) therefore, group selection can only take place in groups with limited dispersal. This argument is based on the assumption that dispersal is random, when in fact random dispersal is more the exception than the rule (Pepper and Smuts 2002, Aktipis 2004, Pepper 2007). When animals base their decision to disperse on the composition of their group, dispersal can increase phenotypic and genetic variation among groups rather than decreasing it. This possibility is supported by both theoretical models (Pepper and Smuts 2002, Aktipis 2004, Pepper 2007) and empirical studies (Eldakar et al. 2009, 2010). Saying that group selection requires limited dispersal mistakenly treats an antiquated argument against group selection as the basic criterion for evaluating group selection.

## *How Confusion About Group Selection is Perpetuated at the Professional Level*

Group selection is often portrayed as a subject that remains controversial after many decades. It would be more accurate to say that group selection remains confusing to many people after many decades. To anyone with a basic understanding of multilevel selection theory, the core question of whether a trait can evolve on the strength of between-group selection, even when selectively disadvantageous within groups, was definitively answered long ago.

It is therefore important to ask how confusion about group selection can persist at the professional level, long after the core issue has been resolved. Imagine submitting an article to a journal or a grant proposal to a funding agency, contemplating whether to explicitly frame your work in terms of group selection. Anticipating the comments that you are likely to receive, it is tempting to avoid using the term, even if group selection is clearly being invoked. Why not frame your work in terms of what evolves in the total population, the group as a social environment, or frequency-dependent selection instead? In this fashion, the received wisdom that social evolution can be explained "without invoking group selection" has appeared to go unchallenged except by a few zealots, when in fact group selection is being invoked in every way except the name.

Ironically, this problem reflects a tragedy of the commons for academic cultural evolution. The individual gains publications and grant proposals that are so vital for career advancement, but the field as a whole suffers from endless confusion about the fundamentals of social evolution. Confusion about group selection at the professional level will end when we eliminate selection against group selection accounts during the review process. We hope that our list of criticisms not to make against group selection will help reviewers and editors alike base their assessments on current knowledge.

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