

Why is group selection such a problem?

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Abstract: The controversy over group selection persists not, as Wilson & Sober argue, because biologists do not understand the hierarchy of vehicles of selection, but because we lack criteria to determine whether or not a trait arises from group selection, and have a deep wish to find a biological basis for our human moral feelings.

Group selection? Still? More? Again? Despite dozens of articles and books on the topic, fundamental disagreements persist. Such intractability usually arises from failure to conceptualize a problem clearly, lack of data, or the influence of political or emotional factors. In the curious case of group selection, all three factors conspire to maintain confusion.

Wilson & Sober (W & S) claim that "overextended definitions of individual and gene selection have misled a generation of biologists into thinking that natural selection almost never occurs at the level of groups" (sect. 1.6) and they set out to "rebuild inclusive fitness theory on the foundation of vehicles" (sect. 1.5). They go to great lengths to show that groups, like individuals, can be vehicles for natural selection. But this is not at issue, is it? Wilson and others have described models in which genes that benefit a group can be selected for even though they decrease an individual's inclusive fitness. These models work, albeit under very restricted conditions. The question is not whether traits that benefit the group at the expense of the individual are possible; the question is whether they are important, and especially whether they can account for human altruism.

This brings us to the paucity of data. The authors use starving rabbits on tiny islands to illustrate the principle, but the lack of evidence for such population limitation is the very spark that kindled the demise of naive group selection. The aberrations from equal sex ratios are intriguing, but no mention is made of alternative explanations for these findings. The Hutterite example, although atypical for the species, proves that humans can be extraordinarily altruistic, but it says nothing about the mechanisms that make this possible, and nothing about the selection processes that shape these mechanisms.

W & S address the core question of whether organisms (especially humans) have traits (especially altruism) that were shaped by the force of selection acting at the group level despite selection against these traits at the individual level. The conceptual problem here seems to me to have little to do with vehicles and everything to do with standards of evidence. How can we tell if a trait arose by this process or some other one? We can not. There is no phylogeny to trace, no comparative information to guide us. If someone could demonstrate a trait that decreased inclusive fitness and increased group fitness, we would have a good start, but I know of no such trait.

As for George Williams, he may have led us out of the wilderness of naive group selectionism, but I doubt that he would endorse the Commandment offered in his name: "Thou shalt not apply the adaptationist program above the level of the individual." Instead, he simply applies Ockham's razor and insists that we explain phenomena at the simplest possible level. He also insists that we carefully distinguish the information (the codex) that is changed by natural selection from the material domains in which that information resides. He notes that, "a gene is not a DNA molecule; it is the transcribable information coded by the molecule . . . a whole addictive organism . . . is not really an object, it is a region in which certain processes take place" (Williams 1992, p. 11). He is well aware that selection can take place at levels other than the genes and the individual. His 1992 book contains some fine examples of clade selection, for example, Van Valen's evidence that individual mammals are selected for larger body size, but clades of mammals with large

bodies are constantly being supplanted by those with smaller bodies.

What about vehicles of selection? The strategy of moving up the hierarchy until one finds fitness differences between vehicles is helpful, but, as the authors say, "fitness differences are not always concentrated at one level of the biological hierarchy. . . . In these cases, we cannot assign the status of organ, organism, or population and must settle for some hybrid designation" (sect. 1.4). Exactly. Except in boring cases, the analogy fails. Viewing selection from the gene's perspective is a great advance precisely because it highlights and explains the complexities that arise when one force of selection favors a gene and another opposes it. Some, but not all, of the best examples arise from conflict between levels of the hierarchy. "Outlaw genes" foster their own success at the expense of the individual. The disadvantage they pose to the individual selects for opposing "police genes," like those that mediate crossing over to separate outlaw genes from their conspirators. The interesting question at the heart of W & S's target article is whether the power of group selection is sufficient to select for genes that cause any appreciable harm to individual inclusive fitness. The consensus has been "probably only rarely." One reason, surprisingly not addressed by the authors, is the fundamental difference between an individual organism and all higher levels of organization. All the cells in the individual share the same genetic information, and thus have their interests in common. Higher-level vehicles have genetic differences, so, in all but the most special circumstances, genes that favor the interests of the group over the individual will be replaced by genes that favor the interests of the individual and its genes.

Conflicts within the level of the individual are equally important because they go further toward replacing the notion of an organism as a perfect creation with a more realistic picture of an organism as a bundle of compromises, and because such conflicts often given rise to disease. In heterozygote advantage, a gene gives enough of an advantage to some individuals to outweigh the disadvantages of disease that arise in other individuals who have two copies of the gene. In antagonistic pleiotropy, a gene offers a benefit and a cost to the same individual. Some, like DR3, increase the likelihood of uterine implantation and retention, but later cause disease, in this case, diabetes. Other genes give a selective advantage in youth that outweighs their later contributions to senescence. Then, of course, there are kin-selected genes that code for behavioral tendencies to assist relatives who share genes identical by descent, thus decreasing the individual's fitness, but increasing inclusive fitness. Although groups in which kin altruism exists may have an advantage over other groups, the fitness differences that select for kin altruism are between individuals, not groups. By contrast, genes that foster reciprocity exchanges impose a cost on an individual in the short run, but give an advantage in the long run (depending on the strategies used by other players and the ability to detect and remember behaviors by others). In all these examples, the conflict is between two effects of the gene in the same individual, or between the effects in two different individuals, not between different levels of the hierarchy.

Enough of conceptual and data problems; what are we to make of the fervor of the quest to demonstrate group selection? W & S seem determined to demonstrate that human altruism arises from group selection. I sympathize with their wish. The discovery that tendencies to altruism are shaped by benefits to genes is one of the most disturbing in the history of science. When I first grasped it, I slept badly for many nights, trying to find some alternative that did not so roughly challenge my sense of good and evil. Understanding this discovery can undermine commitment to morality – it seems silly – to restrain oneself if moral behavior is just another strategy for advancing the interests of one's genes. Some students, I am embarrassed to say, have left my courses with a naive notion of the selfish gene theory that seemed to them to justify selfish behavior, despite

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my best efforts to explain the naturalistic fallacy. Is selfish-gene theory a meme that is toxic to social structures that depend on commitment to abstract moral principles? I worry a lot about this possibility and thus sympathize with those who want to show that human altruism was shaped by group selection. If this were true, it would help, psychologically at least, to reconcile our moral feelings with our biological natures. Unfortunately, it seems to be false.

Nongenetic and non-Darwinian evolution

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The hierarchy of vehicles underlying the main thesis of Wilson & Sober's (W & S's) target article corresponds to the hierarchy underlying so-called organismic system theory, which explores analogical features of structure, function, and evolution of an organism's subsystems (e.g., the cells, tissues, or organs of an individual) and its supersystems (populations, species, ecosystems, groups, societies, nations, etc.).

In the context of human evolution, this exploration is especially relevant to the issues discussed by W & S, because it reveals how our species is unique in a very special sense, namely, we produce and are subjected to an evolutionary process, which is independent of natural selection acting on genes or on vehicles generated by their action.

Consider the taxonomic tree of languages, a direct analogue of the corresponding tree of biological taxa. Both trees portray an evolutionary process. A compelling reason for assuming independence of language evolution from biological determinants is the salience of mechanisms of reproduction and selection apparently unrelated to adaptation in the sense of enhancing the reproduction of genes.

To fix ideas, consider a possible mechanism of the phonetic evolution of a language. Let the phone be the "replicator." Let imitation of the produced phone by other speakers represent reproduction. Let slight changes in the phone play the part of mutations. If the changed phone is easier to pronounce and entails no significant loss of information content, it will be imitated by more speakers and will eventually replace the original one (analogues of differential reproduction rates produced by natural selection). If we suppose that written language is "more conservative" than speech, we can assume that our model is corroborated by the abundance of "silent letters" in English orthography, vestigial parts that have remained functional in German, for example (cf. *Knecht* - knight; *Tochter* - daughter, etc.).

As another example, consider the evolution of artifacts. The "fossil histories" of implements, weapons, articles of clothing, vehicles, and so on can be seen in any museum, revealing striking analogies to the evolution of animals even to vestigial parts. The "horseless carriage" still had a stand for a whip. The automobile "reproduces itself" quite literally on the assembly line. Models that sell well enjoy a reproductive advantage and eventually replace those that do not. Witness the extinct specimens.

Our examples can be regarded as generalizations of Darwinian evolution in the sense that the processes are driven by a kind of reproduction and a kind of selection. They can be called quasi-Darwinian. Evolutionary processes independent of selection based on differential reproduction rates can be called non-Darwinian.

Evolution of systems exemplifies such processes. A system can be defined as a portion of the world that, in spite of far-reaching internal changes, remains "itself." Surely living individuals are examples. Their material constituents are continu-

ally replaced, yet their identities are unmistakable. We humans have direct evidence of our own identity - our memories. There is no difficulty in assuming continued identity of larger organisms, species, groups, organizations, states, even conceptual systems like languages, religions, or scientific theories.

Can one ascribe "adaptation" to such systems, on which their continued existence (preservation of identity) depends? I think we can if we separate adaptation from competition (i.e., differential reproduction rate), the most fundamental concept of Darwinian evolution. This separation justifies calling some evolutionary processes "non-Darwinian" with reference to the level on which differential reproduction rates do not occur. Thus, languages can hardly be said to engage in a survival of the fittest reflected in differential reproduction rates. However, the evolution of a language can be said to be driven by an *internal* quasi-Darwinian process, for example, differential reproduction rates (imitation frequencies) of phones, perhaps also of syntactic and semantic features.

Adaptation of a system to its environment need not be manifested in a superior reproduction rate. It can be evidenced simply by longevity. Successfully adapting systems are still around; those that did not adapt are no longer with us. Consider a firm, an institution, or a religion, that has preserved its identity (is recognized as "itself") for a long time. To say that it has been adapting to its environment is almost a tautology. The interesting question is how. The viability of such a system depends on the support it gets from its environment. A store needs customers, a political party voters, a religion adherents. Support is mobilized by policies, and these are designed and carried out by personnel. Consequently, "adaptation" consists of selecting the personnel recruited into the system. This is the internal analogue of a "Darwinian" process that enhances the survivability of the system by guiding its evolution, which on the higher level appears to be non-Darwinian.

I believe the question of group selection should be defined with reference to the level of analysis. If selection is defined in the strict Darwinian sense, then a case against group selection can be made if the evolutionary success of a group cannot be shown to be a consequence of differential reproduction rates of groups. Survivability of groups (at least human groups) need not depend on reproduction. It does depend on adaptability to environment, however, and this is where the uniquely human repertoire of adaptability methods introduces an entirely new dimension into evolutionary theory.

In directing attention to the vehicle of selection (rather than fixating on the gene as the fundamental replicator), Wilson & Sober open the way to a multilevel theory of selection, thereby providing a theoretical underpinning to group selection. In the context of the evolution of human social behavior and organization, the generalization could go a step further. We can recognize and examine processes that are quasi-Darwinian but not genetic in the sense of being driven by differential reproduction of replicators that are not genes. (Learning may be a further example if we suppose that it is based on differential reinforcement and inhibition of neural circuits.) And we can examine non-Darwinian evolutionary processes - those driven by adaptation to an evolving environment but not by differential reproduction rates.

Adaptation and natural selection: A new look at some old ideas

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Abstract: The debate between individual- and group-selection perspectives centers on the *probability* that group selection played a major role