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Commentary on **David Sloan Wilson and Elliott Sober (1994). Reintroducing group selection to the human behavioral sciences. BBS 17:585–654.**

Abstract of the original article: In both biology and the human sciences, social groups are sometimes treated as adaptive units whose organization cannot be reduced to individual interactions. This group-level view is opposed by a more individualistic one that treats social organization as a byproduct of self-interest. According to biologists, group-level adaptations can evolve only by a process of natural selection at the group level. Most biologists rejected group selection as an important evolutionary force during the 1960s and 1970s but a positive literature began to grow during the 1970s and is rapidly expanding today. We review this recent literature and its implications for human evolutionary biology. We show that the rejection of group selection was based on a misplaced emphasis on genes as "replicators" which is in fact irrelevant to the question of whether groups can be like individuals in their functional organization. The fundamental question is whether social groups and other higher-level entities can be "vehicles" of selection. When this elementary fact is recognized, group selection emerges as an important force in nature and what seem to be competing theories, such as kin selection and reciprocity, reappear as special cases of group selection. The result is a unified theory of natural selection that operates on a nested hierarchy of units. The vehicle-based theory makes it clear that group selection is an important force to consider in human evolution. Humans can facultatively span the full range from self-interested individuals to "organs" of group-level "organisms." Human behavior not only reflects the balance between levels of selection but it can also alter the balance through the construction of social structures that have the effect of reducing fitness differences within groups, concentrating natural selection (and functional organization) at the group level. These social structures and the cognitive abilities that produce them allow group selection to be important even among large groups of unrelated individuals.

Reintroducing "Reintroducing group selection to the human behavioral sciences"to BBS readers

Nicholas S. Thompson

Departments of Biology and Psychology, Clark University, Worcester, MA 01610. **nthompson@clarku.edu**

Abstract: Wilson and Sober's (1994t) revival of group selection theory may have failed with some readers because its simple arithmetic foundation was obscured under the complexities of its presentation. When that uncontrovertible principle is uncovered, it broadens dramatically the fundamental motives that social scientists may impute to human nature and still be consistent with Darwinian evolutionary theory.

Because unnecessary complexity foments confusion, and confusion is the enemy of conceptual change, I am trying to put in the simplest possible form my understanding of the fundamental insight contained in the Wilson and Sober (1994t) target article.

One way to think about their insight is that Wilson & Sober (W&S) show how the bad reputation of group selection for the last 30 years was undeserved, being based on a failure of mathematical intuition on the part of many of their colleagues. One way to describe this failure is that we (sadly, I must include myself in this group) supposed that the mathematical operations appropriate to integers are also appropriate to proportions. Let me illustrate this failure in the simplest possible way. Imagine you have two bags with 100 candy-covered chocolates in each. Imagine that in each bag there are two colors of candy coatings, red and green. Imagine further, that I have a supply of loose red and green candies which I can add to the two bags. Finally, let us imagine that we both prefer the red candies to the green candies.

As a kindness to you (I say), I agree to increase the number of red candies in each of your bags. You rightly accept because you know that if I add some number of red candies to each of your bags, then the number of red candies you have overall must increase.

But now let us say I make a different sort of offer to you: I agree to increase the *proportion* of red candies in each of your bags. Are you assured that I will increase the *proportion* of red candies overall? Well, in fact, no. Imagine that to start with, there are 20% red candies in one bag and 80% red candies in the other. I double the number of candies in the 20%-red bag, giving me 40 red and 160 green, and then substitute two green candies with two red ones, bringing the new proportion of red candies to 21% (42/200). I now halve the number of each kind of candy in the 80%-red bag, giving 40 red and 10 green, and, again, substitute two green candies with two red ones, bringing the new proportion of red candies in this bag to 84% (42/50). Notice that I have, as I promised, increased the proportion of red candies in both bags (20% to 21% and 80% to 84%). But what has happened to the *proportion* of red candies overall? In fact it has *decreased* from 100/200 to 84/250, or approximately 34%.

What does this all have to do with the evolution of sociality? Let there be a population divided into several groups of individuals. Let there also be two kinds of individuals that inhabit these groups, As and Ss: As are group altruists, each of which acts so as to increase the reproduction of its group at its own reproductive expense; Ss are individuals that profit from the activities of As but do not perform any altruistic acts. It follows from these consider-

ations that although the groups with the most altruists have the greatest reproductive success, the proportion of selfish individuals will increase within each group, even those groups with the most altruists. Still, even under these conditions, the proportion of altruists in the overall population may be increasing. And since the evolvability of any trait is determined not by its consequences to its proportion in the groups of which the population is composed, but by its consequences to the proportion of the trait in the population overall, this result means that altruism can be favorably selected in a population divided into groups even if it is decreasing in relative frequency in *every* group in the population.

Essentially, W&S's point is that I and my colleagues have persistently underestimated the possibility of the evolution of group directed altruism in individuals, because we (1) correctly gauged the power of individual selection to reduce the proportion of group altruists in each group and then (2) *incorrectly* assumed that the decrease in proportion within groups entailed a decrease in proportion overall. As W&S have demonstrated, however, it entails no such thing.

If you are an investor, you will recognize that the mathematical principle making group selection a possibility is related to the principle that underlies the success of constant dollar investing. Investors who regularly invest the same amount in a stock will increase the value of their investment *even if the long term value of the stock remains stable.* Why? Because they buy more shares of the stock when it is low and less of it when it is high so that whenever the stock is at its long-term average value, fewer shares have declined to reach that value than shares that have risen to reach it.

I offer this continuing commentary because, after discussing the W&S target article with dozens of colleagues I believe that (1) failure to grasp the simple principle these authors articulate may unnecessarily prolong the methodological individualism that has so cluttered the study of human and animal social evolution for the last two or three decades; and (2) that the welter of arguments, models, and examples in their target article and its associated commentaries may have blinded many of my colleagues to the elementary mathematical fact that underlies their point.

I think it is particularly important for sociobiologists to get clear on this point because of the role that our profession may have played in providing apparent scientific justification for the contemporary individualist Zeitgeist in politics and economics. According to that Zeitgeist, personal or family self interest is the only force that moves human beings and every social good gets translated back into the language of those interests.

But once the W&S insight has been factored in, the evidence of contemporary evolutionary psychology suggests that human individuals are chaos systems constantly teetering between two conflicting behavioral orientations. One we might call the "individualist orientation," which occurs when individuals feel intimately the positive and negative consequences of their own endeavors. We can all think of instances in our own lives and others when people have generated a storm of creative action just because each thing that they got right immediately brought them gains of some sort and each thing that they got wrong immediately brought them losses. The other form of individual organization we might call the "collectivist orientation," which takes over when people cast their lot with other human beings in a group effort, the consequences of which fall more or less equally on all participants. Again, we can all think of cases in which groups of individuals have been amazed at the pleasure and productivity that can arise from such collective efforts.

The reason this insight is an evolutionary psychological one, particularly, is that when the facts and theories recounted in Barkow et al. (1992) are viewed in the context of W&S's group selection theory, it becomes clear that the social behavioral traits of the human species have been determined by selection for both (1) actions that promote the individual's interests regardless of the interests of the group and for (2) actions that promote the interests of the group regardless of the interests of the individual. When, on the one hand, human groupings have happened to be so organized that the consequences of group action fall unequally upon the individuals that make up the groups and the characteristics of individuals as such determine those consequences, then selection has been for individualistic characteristics. When, on the other hand, human groupings have happened to be so organized that consequences of group action fall equally upon them all and characteristics of the group as such determine those consequences, then selection has been for collectivist action by individuals. Because selection has sometimes favored individualistic and at other times collectivist behavior, the human species has evolved not only the capacity for both kinds of action but probably also a complex cognitive device for figuring out in a given situation which kind of action, collective or individualistic, is likely to produce the best genetic outcome.

What this means is that whenever human beings get together into groups, the individuals in them are constantly trying to assess what sort of a group they find themselves in: Is this a group in which collective action is likely to produce the best result or is it a group in which individual action is likely to produce the best result? If their assessment is that collective action will be most productive, then the individuals will cast their lot with the group, and you may see people making genuinely self-sacrificial offers to benefit group achievement; if, on the other hand, their assessment is that individual action will be the most beneficial, then you will see people asserting individual interests regardless of the consequences to group achievement. The theory also predicts that in the latter case people are likely to try to deceive themselves and others about the nature of the situation and to convince others that a genuine collective interest exists, while continuing to act in their own individual interest. None of these behavioral tendencies, need, of course, be conscious in any way.

These insights obviously have tremendous implications for our social and political lives and for the design of our communities. Because of their significance, we cannot tolerate further delay in their consideration, delay that arises from the still wide-spread belief that group selection is impossible in human populations.

ACKNOWLEDGMENT

I wish to thank all the colleagues at the recent annual meetings of the Animal Behavior Society in Flagstaff, AZ, who helped me as I tried to work through the implications of Wilson and Sober's original BBS target article for my research and teaching program in ethology. I am particularly grateful to Elliott Sober and David Sloan Wilson for their patient e-mail correspondence and for the privilege of reviewing an early draft of their upcoming book, *Unto others: The evolution and psychology of unselfish behavior.*

Authors' Response

Multilevel selection and the return of group-level functionalism

David Sloan Wilson[a] and Elliott Sober[b]

[a]*Department of Biological Sciences, Binghamton University, Binghamton, NY 13902-6000;* **dwilson@binghamton.edu**

[b]*Department of Philosophy, University of Wisconsin, Madison, WI 53706;* **ersober@facstaff.wisc.edu**

Abstract: We reinforce **Thompson's** points by providing a second example of the paradox that makes group selection appear counterintuitive and by discussing the wider implications of multilevel selection theory.

We thank **Thompson** for clarifying some of the subtleties of multilevel selection theory, which may have been lost in

the complexity of our target article. The fact that local changes in frequency do not always predict global changes is known as Simpson's paradox (Simpson 1951; discussed in Sober 1984; 1993; Sober & Wilson 1998). It might help to supplement Thompson's candy example with another example to illustrate the counterintuitive nature of the paradox. During the 1970s, the University of California at Berkeley was suspected of discriminating against women in its graduate admission policies (Cartwright 1979). The percentage of women applicants who were admitted was less than the percentage of men, and the difference was large enough that it could not be attributed to chance. The University conducted a department by department inquiry, but found in each department that women were admitted no less often than men. Evidently, women did worse than men overall, but not in any department.

This paradoxical finding fell into place when it was noticed that women tended to apply to departments with low acceptance rates. To see how this can happen, imagine that 90 women and 10 men apply to a department with a 30% acceptance rate. This department does not discriminate and therefore accepts 27 women and 3 men. A second department with a 60% acceptance rate receives applications from 10 women and 90 men. This department doesn't discriminate either and therefore accepts 6 women and 54 men. Considering both departments together, 100 men and 100 women applied, but only 33 women were accepted, compared to 60 men. A bias exists in the two departments combined, despite the fact that it does not exist in any single department, because the departments contribute unequally to the total number of applicants who are accepted. In just the same way, altruists can increase in frequency in a global population, despite the fact that they decrease in frequency within each group, because the groups contribute unequally to the total number of offspring.

Despite the counterintuitive nature of these examples, it is easy to check for the presence of group selection in a mathematical model or a biological example of evolution. One simply compares evolutionary changes at the local and global level, the way that Berkeley compared admission rates at the level of single departments and the entire University. If a trait (or a gene that codes for the trait) declines in frequency at the local level but increases in frequency at the global level, that is a sign that the trait evolves by group selection. When this simple test is applied to theoretical and empirical developments in evolutionary biology during the last 30 years, it can be shown that group selection has been invoked many times by those who think they have rejected it (see Sober & Wilson 1998 for a more detailed account).

We also agree with **Thompson** that the premature rejection of group selection contributed to the decline of a much larger intellectual tradition in which higher-level entities (groups, societies, cultures, ecosystems) are regarded as organismic units in their own right, as opposed to mere collections of self-interested individuals. This tradition has always been strong in everyday thought and was well represented in biology and the human behavioral sciences through the first half of this century. According to the psychologist D. M. Wegner (1986 p. 185),

> Social commentators once found it very useful to analyze the behavior of groups by the same expedient used in analyzing the behavior of individuals. The group, like the person, was assumed to be sentient, to have a form of mental activity that guides action. Rousseau (1767) and Hegel (1807) were the early architects of this form of analysis, and it became so widely used in the nineteenth and early twentieth centuries that almost every early social theorist we now recognize as a contributor to modern social psychology held a similar view.

The decline of group-level functionalism can be traced to a number of factors (an excellent topic for historians of science), but among them was a conclusion that seemed to emerge from evolutionary biology – that groups should almost never be regarded as anything more than a collection of individuals pursuing their separate reproductive interests. This conclusion was especially devastating because it appeared to be based on theoretical considerations, as opposed to the more practical considerations that form the basis of methodological individualism in the human sciences. A psychologist might argue that the group-level perspective is unproductive, but an evolutionary biologist could argue that it is just plain wrong. The most important implication of multilevel selection theory is therefore to reinvigorate the group-level perspective across a broad range of academic disciplines. This does not mean that social groups and other higher-level entities can always be regarded as organismic units. We have never argued that group selection is all-important and such an argument could not be sustained. But it does mean that the concept of adaptation can be applied to higher-level entities with suitable caution and that group selection may have been an exceptionally strong force in human evolution, explaining a groupish side to human nature that has been obscured during recent intellectual history by the individualistic perspective.

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The letter "r" appearing before the author's initials refers to the response to the continuing commentary.

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