



BOOKS: EVOLUTION OF BEHAVIOR

Are We Selfish, Are We Nice, or Are We Nice Because We Are Selfish?

Leonard Nunney

Unselfish action is a hallmark of humanity. We may sacrifice our lives for the good of our children, for the good of our nation, and sometimes even for the good of a stranger. What motivates such altruistic acts? To a biologist, this question has two very different answers. There is the proximate answer that explains our psychological reasons for acting altruistically, and there is the ultimate answer that explains how an unselfish act increases our Darwinian fitness relative to some selfish alternative. Through the two more-or-less independent sections of *Unto Others*, Sober and Wilson discuss both proximate and ultimate explanations. They use both sections to also emphasize their belief in the value of pluralistic hypotheses, with natural selection driven by multiple levels of causation and behavior driven by multiple desires.

The book's cover proclaims that the authors "demonstrate once and for all that unselfish behavior is in fact an important feature of both biological and human nature." Specific examples of altruistic behavior from many animals are well established; I was intrigued, however, to see if the authors would provide definitive scientific evidence of a much broader role for altruism. Certainly, demonstrating the evolution of altruism in human populations is not an easy task. For this reason, I was most interested in the validity of the science, rather than the eloquence of the arguments.

The evolutionary argument is presented in the first five chapters. The authors conclude that: "At the behavioral level, it is likely that much of what people have evolved to

do is *for the benefit of the group*" (p. 194). Their italics emphasize their view that these behaviors could not evolve by individual selection, since much of our behavioral repertoire appears to be altruistic—disadvantageous for the individual but advantageous for the group. Anyone who has studied developments in evolutionary biology over the last 30 years knows that this is a provocative statement. Special conditions (such as close kinship or long-term group isolation) must be satisfied for natural selection to favor the benefit of the group over the benefit of the individual. Nevertheless, I see no reason why such special conditions could not prevail in at least some human cultures. So the authors' tasks were to present data and lead us logically from the data to the conclusion that group selection is acting on altruistic traits. Unfortunately, the authors get bogged down in the history of the group

for analyzing natural selection in spatially structured populations (2). In real populations, individuals interact with their neighbors (rather than randomly interacting with all members of the population), and in his book Wilson examined some of the evolutionary consequences of this reality. Unfortunately, he folded this valuable insight into the debates over group selection and the evolution of altruism, with the result that individual selection in spatially structured environments and group selection became—in Wilson's view—indistinguishable. This fusion continues to play a central role in *Unto Others*, with the authors finding altruism abundant in nature mainly because of the way they define it.

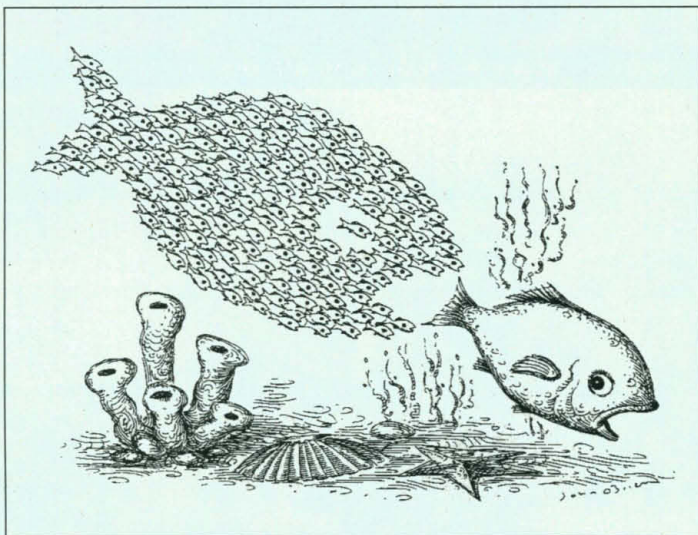
Consider the following example (3) in which money substitutes for fitness. You are given a choice. Either you can receive \$10 and keep it all, or you can receive \$10 million if you give \$6 million to your next-door neighbor. Which would you do? Guessing that most selfish people would be happy with a net gain of \$4 million, I consider the second option to be a form of selfish behavior in which a neighbor gains an incidental benefit. I have termed such selfish behavior benevolent, while Sober and Wilson consider the behavior altruistic. To them, only the individual taking the \$10 would be acting selfishly.

This example is important because it parallels one heavily emphasized in the book to justify the generality of group selection and altruism, the production of the Hamiltonian female-biased sex ratios (4). Such biased sex ratios are commonly produced by female parasitoid wasps, which (by virtue of male haploidy) have complete control over the sex ratio of their brood. Sober and Wilson define such females as altruists, and yet these females are actually making a choice that is the biological equivalent of taking the \$4 million instead of the \$10. Sober and Wilson do not mention this alternative perspective; hence selfish (but benevolent) traits, which require no special conditions for their persistence except spatial structure, are never separated from the truly altruistic traits that are always vulnerable to the invasion of selfish cheaters. The authors' failure to make this important distinction does major disservice to their avowed goal of pluralism.

Sober and Wilson compound the difficulty by applying group selection with the same broad brush: "Group selection favors any behavior that increases the relative fit-

selection debate and pay little attention to the scientific goals. They attempt to convince the reader that a scientific revolution is needed before evolutionary biologists will recognize the importance of multi-level selection theory. But such theory is already extensively applied in ways that enhance our understanding of gene frequency change; kin selection and gametic selection are examples that have been recognized for many years (1).

In 1980 Wilson published an important book in which he presented a framework



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ness of groups" (p. 30). Unfortunately this approach promotes confusion between the traditional concept of group selection advanced by Williams and Maynard Smith, and Wright's concept of interdemic selection, which focuses on spatial structure. Sober and Wilson move from the overkill of the 1960s, when nothing was attributed to group selection, to a position where almost everything could be. In fact, their approach leads to the conclusion that almost all interactions affecting fitness (such as competition) invoke group selection. For example, using their definition, the effects of competition among randomly sown seedlings in a field must include components of group and individual selection. I fail to see how such partitioning improves our understanding of the evolution of competitive ability; rather, I suspect that their method generally decreases our ability to see simple patterns.

The traditional concept of group selection demonstrated that interactions must occur preferentially among similar genotypes for altruism to evolve (3), a point tacitly recognized in the section on "assortative interactions." The classic (hypothetical) example of such interactions is not mentioned: the green-beard effect. Dawkins (5) suggested that if an altruism gene caused its carriers to have a green beard, then directing altruism to green-bearded individuals would allow the trait to spread in the absence of the more usual assortative mechanism of kinship. This example also illustrates that altruists are vulnerable to a selfish cheat that dyes his beard green. Sober and Wilson make the valid point that cheating in human society may be difficult, primarily because individuals accumulate a long history of interactions. In developing their argument they invoke what they call "primary" behaviors and "secondary" behaviors, but in doing so they reinvent the logic of traditional group

selection that they had previously criticized so heavily. Translated into conventional terms, primary behaviors are altruistic acts and secondary behaviors are policing mechanisms that prevent cheating. The new terminology does nothing to clarify the issues, as can be seen from the following passage: "When a secondary behavior is used to promote a primary behavior that would otherwise be altruistic, the secondary behavior is also altruistic from the evolutionary perspective" (p. 145).

In the fifth chapter, the centerpiece of the evolutionary story, the authors apply data from human cultures to support their ideas. Unfortunately, as the authors themselves note, the analysis is preliminary and in the form of just-so stories. In addition, Sober and Wilson fail to present criteria for distinguishing altruism spreading through non-familial group selection from that spreading by kin selection, reciprocal altruism, or other mechanisms. They shift without apparent concern from adaptive genetic arguments to adaptive cultural arguments, and conclude that "social norms function largely ... to make human groups function as adaptive units, even when their members are not closely related" (p. 173). We all have preconceptions, but I am concerned that Sober and Wilson allow theirs to dominate their argument: "human social groups are so well designed at the group level that they must have evolved by group selection" (p. 191). I agree that group selection operates on culture; human history is full of examples of one group taking over another and imposing its culture. But is this the evolution of altruism? More likely, the relevant cultural difference is the ability to wage war. The authors' shift to cultural evolution is made with deceptive ease, and I was left with the impression that the framework of cultural transmission needs to be much more clearly defined.

In particular, cultural traits can be complex (pleiotropic) and can spread instantly from rarity to fixation by edict. These features make the definition and dynamics of cultural traits quite different from single gene effects.

The second half of the book brings to mind the old Monty Python cliché, "And now for something completely different." These five chapters focus on a single ques-

tion: Do people act unselfishly because they have a desire to be altruistic (Sober and Wilson's pluralistic hypothesis) or because the altruistic act satisfies some selfish desire for, say, pleasure or the avoidance of pain (the egoism hypothesis)? The authors discuss some experiments purporting to separate these alternatives, although it is not clear, even to them, that the problem can be approached scientifically using currently available techniques. Unfortunately, the expected outcomes are debatable, and I suspect that the statistical testing is further compromised by disagreement over the choice of the null hypothesis. The authors argue that a pluralistic model including both selfishness and altruism should have this role, but I can see why this would not be universally accepted.

This section of the book offers an interesting insight into a philosopher's approach, and I found many of the arguments enjoyable. But I am not persuaded that reality can be logically deduced using a philosophical lexicon. More to the point, I was unconvinced by the attempt to use evolutionary arguments to distinguish between egoism and pluralism. Certainly the authors can have their own opinion: "motivational pluralism, we believe, has a higher degree of evolutionary plausibility" (p. 324). This belief does not, however, justify the view that the evolutionary perspective resolves the choice between these two hypotheses.

Sober and Wilson end by concluding that pluralism is important, both in the study of natural selection and in the study of psychological motivation. They have the laudable goal of stimulating research into levels of selection and motivation as applied to humans and their culture. Although I agree with much of what the authors say and what they hope to achieve, this book is more focused on debate than science. The book's two long arguments are interesting when viewed as such, but anyone looking for novel scientific insight will be sadly disappointed. And what of pluralism? I cannot imagine that many readers would have any strong disagreement with a pluralistic approach to the problems of human life and culture. From a scientific perspective, however, my response is that pluralism is good when it is necessary, but sometimes it is just not necessary.

References

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VIGNETTE

Environmental Expertise

By statured scientists I mean those who collect and analyze the data, build the theoretical models, interpret the results, and publish articles vetted for professional journals by other experts, often including their rivals. I do not mean ... the many journalists, talk-show hosts, and think-tank polemicists who also address the environment, even though their opinions reach a vastly larger audience. This is not to devalue their professions, which have separate high standards, only to suggest that there are better-qualified sources to consult for factual information about the environment. Seen in this light, the environment is much less a controversial subject than suggested by routine coverage in the media.

—Edward O. Wilson

in *Consilience: The Unity of Knowledge* (Knopf, 1998)