

SPECIAL DEBATE ON GROUP SELECTION AND THE EVOLUTION OF ALTRUISM

The hottest topics in evolutionary science today are evolutionary psychology, evolutionary ethics, and the origins of virtue and altruistic behavior. How would natural selection produce unselfish behavior? In a controversial new book, *Unto Others: The Evolution and Psychology of Unselfish Behavior* (Harvard University Press), philosopher Elliott Sober and biologist David Sloan Wilson propose a modified theory of group selection, a concept long thought dead in the field but now revived with new evidence and new mathematical models.

Because of the importance and interest in this subject, we asked Robert Trivers, who pioneered the scientific study of cooperative social behavior using strictly Darwinian selective forces, to review the book for SKEPTIC. A long-time skeptic of group selection, Trivers' review is strongly critical of Sober and Wilson. Therefore, we invited Sober and Wilson to defend themselves and their book. As is customary in such matters, we allowed Trivers the final word. So read Sober and Wilson's book and enjoy this lively exchange between some of the leading evolutionary thinkers of our time in this debate on how and why humans became the moral animal. —Editors

AS THEY WOULD DO TO YOU

A review of *Unto Others: The Evolution and Psychology of Unselfish Behavior*.

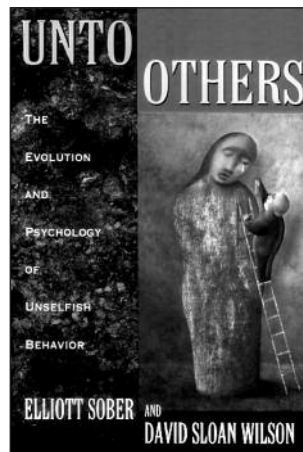
By Elliott Sober and David Sloan Wilson. 1998. Harvard University Press. ISBN: 0-674-93046-0

Robert Trivers

THIS IS A THOROUGHLY disappointing book, start to finish. It is alternatively aggressive and defensive, promising too much and achieving too little. It is entirely too willing to indulge in asides, to consume time with trivial matters, to postpone gratification and to confuse semantic obfuscation with theoretical advance. You know you are on the slow train to nowhere when, in a book promising to treat the evolution and psychology of unselfish behavior, we have time on p. 252 to stop and consider whether *introspection* may provide an adequate evidentiary basis for firm conclusions on human behavior?! If the answer to that is "yes," I want off this train. As it is, I wish I were reading a different book on the train.

Part of the problem the authors have is that they would like to have the respectability of rigorous group selection thinking while at the same time having the breadth and scope of the discredited, old-fashioned group selection thinking. This causes them, on the one hand, to play verbal tricks designed to enlarge the apparent scope of "group selection" and, on the other hand, to almost immediately limit their exploration of the mathematical consequences of a rigorous formulation, precisely because (I believe) this would show that group selection *sensu strictu* is expected to be a very minor selective force in most species, most of the time.

An example of the first case is their subsuming kin selection as a form of group selection (with considerable loss of power, since degree of relatedness r drops out, as do Hamilton's handy rules, e.g. $B > C$ for positive selection of altruistic acts, where B is benefit conferred and C cost suffered). In short, they have rendered kin selection both abstract and impotent at the same time, but this is a virtue because it permits them, along with some additional assumptions detailed below, to close



out the first half of the book with the astonishing statement that "At the behavioral level, it is likely that much of what people have evolved to do is *for the benefit of the group*."

As an example of the second case, that is, failing to pursue rigorous formulation, they rightfully push forward the work of George Price and his variance/co-variance equations for natural selection, equations that can be expanded infinitely on one side to encompass ever greater units of selection. But an important feature of these equations is that the power of each new term is usually an order of magnitude weaker than the previous one. This is

certainly true for intragenomic conflict compared to individual selection, where selection coefficients of 50% during meiotic drive, for example, give way to 5% or weaker selection coefficients for individual selection. With even very modest degrees of migration between groups, a similar weakening is expected as we move from individual to group selection, but migration and dispersal, key subjects for any clear, quantitative treatment of group selection, are all but absent from this book.

I was surprised to see that the first two major examples of group selection chosen for discussion were two cases I thought I understood perfectly well without reference to group selection; namely, selection for female-biased sex ratios under inbreeding, and selection for attenuation of parasite virulence, especially when hosts are infected by single streams of parasites. Under outbreeding, selection favors the production of 1:1 sex ratios, but under inbreeding—specifically sibmating—there is selection on females to economize in the production of males since these now become partly redundant from her standpoint (they will compete with each other for access to sisters). As

W.D. Hamilton showed in 1967, it is easy to solve the general problem of how biased the sex ratio is expected to be, with a given frequency of sib-mating, by measuring only a female's expected number of grandchildren. The problem can be recast in the language of group selection but the problem was solved without use of such language.

When multiple strains of a parasite infect a host, they will be in competition with each other to maximize reproductive output but this will tend to have a negative effect on host survival and thereby parasite survival. Some balance will be struck and one can think of the balance as being between group selection acting at the level of host survival and individual selection acting at the level of competing strains of the parasite. Nothing wrong with this formulation but I thought I understood the competition very well without breathing the language of group selection over a problem that was easily formulated, and solved, in conventional terms. Once again, I have learned nothing from this example I did not know already.

But these are Sober and Wilson's strong suits. When they come to human beings, and most of the book is about human beings, evidence tends to disappear entirely. Except for a very welcome 20 pages mid-book that review some relevant facts from a sample of human cultures, there is no effort to make a sustained empirical contribution. Chapter 8 is called "Psychological Evidence" and I eagerly turned to it first, hoping to find psychological evidence of group selection acting on humans, although I could not easily visualize the form such evidence might take. Given selection for deceit and self-deception, for example, psychological evidence alone would seem at best equivocal, but in any case no evidence whatsoever is presented in this chapter. Well, perhaps the chapter at least defines precisely what the evidence would look like if it existed? Nothing of the sort. It simply ruminates on some of the problems that arise when one starts to think about possible psychological evidence. This is delayed gratification followed by no gratification.

The later philosophical chapters, presumably mostly written by Sober (a professor of philosophy at the University of Wisconsin; Wilson is a professor of biology at Binghamton University), did not seem to me to be especially useful. In fact, they prompt the thought that philosophy is much better at obscuring reality than it is at explicating it, at confusing rather than clarifying, however much philosophers may justify their activity on the opposite assumption. To me it seems mostly a waste of time to consider various philosophical doctrines like Hedonism or Egoism. The effort to put together a coherent theory of psychology using terms such as desires, thoughts and beliefs seems to me doomed at the outset. One would be much better off to begin with the assumption that the brain and mental activities are broken into functional modules, as evolutionary psychologists are fond of putting it, which of course are hierarchically and otherwise organized but which nevertheless can direct purposive activity without requiring one simple, all-encompassing rule like "pursue pleasure and avoid pain in all situations." To take but a simple example, if you fling yourself in front of an automobile to save your own child it is hard to see how you are

at that moment choosing the more pleasurable and less painful alternative, yet it is easy to imagine that such behavior could be favored by natural selection. It hardly seems an intellectual advance to argue that the real reason you jump in front of the car is that you wish to avoid the guilty feelings that would torment you for many years if you survived and your child did not and so you are, indeed, choosing the less painful of two options. But this is the kind of argumentation you are forced into if you adhere to two- and three- and four-hundred-year-old styles of thinking about mental activities.

Curiously enough, Sober and Wilson fail to discuss the one human behavior that conventional evolutionists imagine might easily be affected by group selection, namely genocidal warfare. Here we may see "unselfish" behavior at its best, groups of human beings cooperating to their delight in the complete obliteration of their neighbors. We have strong group effects and an undeniable record of their frequency in human history, from biblical times to the present. But focussed as they are on within-group altruism, Sober and Wilson seem not to see its ugly between-group twin.

Sober and Wilson repeatedly make the claim that the group selection alternative is slighted in modern biology out of ignorance and prejudice. I believe that lack of accomplishment is now the main reason. It may be my old age, but I prefer not to give up well-trod and well-proven ways of thinking about social phenomena for alternative ways unless the new ways reinterpret old phenomena or explain new evidence. Sober and Wilson's real examples of group selection are examples of group selection under highly particular (and, I might add, easily understood) conditions. The rest of their effort is an attempt to convince us that group selection is a globally important process and, indeed, the major selective factor molding all of human behavior. They can make this claim only by reinterpreting kin-selection as a form of group selection, treating reciprocal altruism as a form of group selection, calling all instances of social interaction between individuals, however fleeting or few their number, examples of groups and hence acted upon by group selection, and then by failing to explore in a rational way, or indeed at all, the *power* of group selection—given even low levels of between-group migration—compared to the power of individual or genic selection. The second half of the book presents precious little in the way of factual evidence and makes no obvious advances in describing the kinds of factual evidence needed.

Unto Others brought to mind two visits to my office when I was a young professor at Harvard in the 1970s. The first was from a freshman in my "Social Evolution" class. He said that he was disturbed by the implications of natural selection applied to human behavior. I seemed to be arguing, he said, that there were only two kinds of altruism in nature, kin-directed and return-benefit, chiefly reciprocal altruism. He asked if I thought there was any other kind of altruism out there. I said I did, and his face brightened and he asked me what its meaning was and I said it was being selected out. His face fell and, as he stood up to leave, he said he could not go on living believ-

ing the things I believed. I smiled broadly and assured him that it created no problems for me at all! I suppose it was a trifle cruel on my part and now, slightly more sophisticated perhaps, I could hold out a little bit of Wilsonian group selection to hang his hopes on. I could tell him that there was probably some additional human altruism that was explained by group selection but exactly what it was, where you would find it, and how you would know that it was there, had not yet been solved.

The second visitor to my office was a young post-doc full of enthusiasm for a more sophisticated kind of group selection thinking than the old discredited form. He said he wanted to devote himself to exploring the legitimate and defensible group selection. I begged him not to do so. There were so many fascinating and important problems remaining to be solved using good old individual selection reasoning, while group selection by necessity had to be found in nature but would be limited, so I told him, to very special circumstances, very

special life cycles, unusual constraints on migration, and so on. I even tried to blow a little smoke up his ass, so to speak, and told him it was obvious that he was bright and that with his theoretical talents he might make major contributions to biology while a life spent on group selection would inevitably come up short. That visitor, of course, was David Sloan Wilson. He obviously followed not a word of my advice. Nor have things turned out quite as I predicted. He has not been reduced to talking about extreme life cycles and special circumstances. Quite the contrary. He has maintained his vision of group selection as an intrinsically important evolutionary phenomenon, especially when applied to humans. But for my tastes, this vision has come at a cost, by blurring distinctions that are better kept bold, by failing to identify precisely the circumstances under which one would expect group selection to be important and what effects it should produce and by a complete failure, as I see it, to enrich our understanding of real phenomena in nature, both inside our species and out.

THE GOLDEN RULE OF GROUP SELECTION

REPLY TO ROBERT TRIVERS' REVIEW OF *UNTO OTHERS*
DAVID SLOAN WILSON AND ELLIOTT SOBER

UNTO OTHERS (UO) CHALLENGES A TRADITION in biology, the social sciences, and everyday life that interprets all behaviors and motives as ultimately selfish. Robert Trivers was one of the architects of this tradition in biology, so perhaps his dismal review is not surprising. Other reviewers have called UO "one of the most important books of the decade" (*Trends in Ecology and Evolution*, v 11 p. 467, 1998) and "the final knell of the group selection controversy" (*Managerial and Decision Economics*, in press). Reviews have so far been strongly polarized, as one might expect from the controversial nature of our subject, so in the spirit of objectivity at the end of our reply we have provided excerpts of all published reviews on UO's Amazon.com web page, including the negative ones.

Trivers hasn't even written a good bad review because he fails to describe the content of what he criticizes. The first half of UO describes a theory of evolution called multilevel selection, which explains how groups and even ecosystems can be like organisms in the harmony and coordination of their parts. Just as organs evolve to benefit the individual, so individuals can evolve to benefit their group. Multilevel selection became a heretical concept in the 1960s; we argue that its rejection was premature and that group selection has probably been a strong force in human evolution. The organismic view of human society, expressed across cultures and throughout history, is more than a fanciful metaphor and can be justified scientifically. This is the claim that Trivers, viewing the world through his individualistic lens, calls "astonishing."

The second half of UO explores the motives that cause people to behave as they do. Why are all behaviors, helpful and harmful alike,

often attributed to ultimately selfish motives, as if genuinely altruistic impulses are a figment of the romantic imagination? We show that this influential view of human nature is bolstered mostly by an arbitrary intellectual pecking order in which defenders of altruism must *prove* their case while defenders of egoism merely have to *imagine* conceivable possibilities. When altruistic and egoistic motives are allowed to compete on the even playing field of evolutionary theory, a form of pluralism that includes both emerges as the probable winner.

The two halves of UO are loosely connected, not because of inattention on our part, but because of the nature of the subject. The evolution of a behavior (Part 1) says little about the proximate mechanisms that evolve to motivate the behavior (Part 2). Group selection can evolve helping behaviors that individuals produce via mechanisms that are psychologically egoistic. Individual selection can evolve self-serving behaviors that individuals produce via mechanisms that are psychologically altruistic. The concepts of selfishness in evolution and psychology are often thought to be equivalent and interchangeable. We show how different they are, which we think is an important strength of our book.

Now that we have described the content of UO, we will attempt to diagnose Trivers' allergic reaction. One amusing symptom is that he denies the importance of group selection in human evolution when it leads to constructive outcomes (altruism within groups), but accepts its importance when it leads to destructive outcomes (genocidal warfare among groups). In fact, these are two sides of the same coin that must be considered together. Trivers states that we ignore the dark side of the coin. On the contrary, our inquiry begins with

Charles Darwin, the first group selectionist, who imagined human tribes supplanting other tribes. We reject naively romantic views of human nature in the Introduction (p. 9) and provide an extended example of intertribal warfare in Chapter 5 (pp. 186-191). Most readers will discover both sides of the coin in *UO*, even if Trivers did not. The most that group selection can do is turn groups into superorganisms. We already know the harm that organisms do to each other and no less can be expected of superorganisms. At the same time, natural selection is not always of the tooth-and-claw variety. Plants evolve exquisite adaptations to survive in the desert without directly interfering with other plants (an example used by Darwin), and groups can evolve into adaptive units without directly interfering with other groups. Intergroup conflict can be underemphasized, but it also can be overemphasized. Now that we have acknowledged the dark side of the group selection coin, perhaps Trivers can strive for logical consistency by acknowledging that there *is* a coin.

Science is often portrayed as an efficient process that cuts quickly to the truth. Alas, all too often it is like the three stooges trying to move a piano. The twists and turns of science are fascinating in their own right and *UO* includes by far the most detailed history of the group selection controversy that has been published. There is an element of real progress—the piano does get moved—but there are plenty of heads knocking together like coconuts along the way. Trivers largely ignores our account in favor of one that is like the school version of American history in which our government can do no wrong. In this account there is an evil theory called group selection that is slain by two shining knight theories called kin selection and reciprocity. The memory of the evil theory must be preserved as an example of how not to think, but now the whole black-and-white picture is being obscured by a talented-but-misguided scientist who has the nerve to insist that group selection not only lives but incorporates kin selection and reciprocity as special cases. This person operates all by himself, like the Lone Ranger, assisted by his trusty philosophical companion, Tonto. If his confusions are allowed to spread, his well-meaning efforts can only end in disaster. If only he had listened to the sage advice of the young Harvard professor who urged him to direct his talents elsewhere!

Now really. Anyone who felt the urge to go beyond their American history textbook must feel a similar urge to go beyond this myth to a deeper historical and conceptual understanding of the group selection controversy. *UO* is the place to start. Instead of the Lone Ranger, the reader will encounter the work of a sizable community of respected scientists who regard multilevel selection as an established fact and a productive research program. Some aspects of our account may be wrong but challenges must go beyond repetition of the myth. In this connection, it is interesting that two of the most influential critics of group selection in the 1960s, G. C. Williams and W.D. Hamilton, both later revised their views and acknowledged the significance of group selection, as we describe in Chapters 1 and 2 of *UO* (neither Williams nor Hamilton have commented in print on *UO* and we do not wish to imply that they agree with us in every respect).

Critics of group selection, like Trivers, continue to invoke the authority of Williams' and Hamilton's earlier work, but are curiously silent on what they said later.

The blows that Trivers rains upon our book painfully contradict each other and at times he seems to be slugging himself. First he accepts the Price equation as a proper model of multilevel selection. Then he claims to understand sex ratio and parasite virulence without recourse to group selection. What he doesn't say is that these traits are commonly analyzed with the Price equation, which reveals an important component of group selection! Trivers also fails to mention that Hamilton used the Price equation to reformulate his theory of inclusive fitness, revealing that altruism among kin evolves by group selection. As a technical aside, the coefficient of relatedness does not disappear from the Price equation but instead becomes reinterpreted more generally as a degree of correlation between the genotype of the individual and the average genetic composition of its group. In short, when Trivers argues that female-biased sex ratios, reduced virulence in disease organisms, and kin selection are not examples of group selection, he is arguing against Hamilton, Williams, and many other scientists in addition to ourselves. By portraying us as the Lone Ranger and Tonto, he seriously distorts his own field of evolutionary biology. Finally, Trivers claims that each level of selection is progressively weaker; coefficients of 50% for selection between genes within individuals, only 5% for selection between individuals within groups, and presumably much lower for selection between groups within the global population. By this logic, how can *individuals* evolve into adaptive units, which entails selection between individuals prevailing over selection within individuals? And where did Trivers obtain these estimates of the general magnitude of different levels of selection? We suspect that he simply asserts them as fact because they strike him as plausible.

The “now I see it, now I don't” quality of Trivers' review is characteristic of the entire group selection controversy. We call the core problem “the averaging fallacy,” which Trivers does not mention in his review, even to criticize it. The averaging fallacy labels any trait that evolves *self-interested*, even when many groups are present, fitness differences exist within and among groups, and the between-group component is responsible for the evolution of the trait. Group selection is no longer a process that is theoretically possible but unimportant in nature; it simply is defined out of existence. Trivers' account of sex ratio and disease avirulence provides two examples of this disappearing act, which Chapter 1 of *UO* describes in much greater detail, but the best example of the averaging fallacy is the concept of the selfish gene. A gene can succeed at the expense of other genes in the same individual, or it can succeed by helping the individual in which it lives to perform better than other individuals. Both count as examples of so-called “gene selfishness” but they are importantly different. In the first case the gene interferes with the adaptive design of individuals (e.g. by causing cancer, meiotic drive, and other forms of intragenomic conflict), while in the second the gene contributes to the adaptive design of indi-

viduals, resulting in organisms in the conventional sense of the word. A selfish gene theorist might say that he can explain everything—even why individuals are complex and well organized—by selection at the gene level and without recourse to individual-level selection. Perhaps, but the claim succeeds only by calling the standard concept of individual selection (the differential survival and reproduction of individuals) a form of gene selection. Furthermore, calling it gene selection does not entail a denial of individuals as adaptive units (which are labeled “vehicles of selection” in selfish gene theory).

In the same way, individuals can succeed at the expense of other individuals in their group, or they can succeed by causing their group to perform better than other groups. Both count as examples of so-called “individual selfishness” as far as Trivers is concerned but in the first case the individual interferes with the adaptive design of its group while in the second it contributes to group-level adaptive design. Trivers might say that he can explain everything—even why groups are complex and well organized—without recourse to group-level selection. Perhaps, but the claim succeeds only by calling the standard concept of group selection (the differential survival and reproduction of groups) a form of individual selection. Furthermore, calling it individual selection does not entail a denial of groups as adaptive units, the very claim that Trivers regards as “astonishing.” This facile argument that group-adaptation-is-really-individual-adaptation-is-really-gene-adaptation produces the hollow sound of coconuts that UO was written to reveal and avoid.

Trivers accuses us of playing semantic tricks but it is the averaging fallacy (which Trivers commits without defending) that is the trickster. By denying the reality of group-level adaptations merely by relabeling them as examples of individual selfishness, which in turn are relabeled as examples of gene selfishness, higher levels of selection are defined out of existence—a cheap victory for the individual and gene selectionist, but the only one available. The beauty of multilevel selection theory is its partitioning of selection into *mutually exclusive* components: between genes/within individuals, between individuals/within groups, and between groups/within the global population. This partitioning reveals between-group selection as an important evolutionary force, especially in our own species.

As we mentioned earlier, it is essential to separate the question of why a behavior evolves from the question of what mechanism inside the individual causes that behavior to occur. Sunflowers turn towards the sun. The evolutionary explanation for why they do so is that the sun is a source of energy. But this point does not address the question of proximate mechanism—what piece of machinery inside the flower makes it turn? It would be a silly mistake to say that since we understand why phototropism evolved, it is a waste of time to ask what proximate mechanism inside the flowers makes them turn. Yet this is precisely the mistake we find in Trivers’ comments on the second part of UO, which discusses the question of psychological motivation. Why do parents rescue their children when they are about to be run over by a car? Trivers says that natural selection has caused the

behavior to evolve, and concludes that it is a waste of time to consider whether parents are egoists or altruists (or both) in their psychological motivation. If Trivers is not interested in such questions, that, of course, is his prerogative. But psychologists, as well as many others, are interested in psychological questions of motivation. Trivers is wrong to think that their questions have already been answered or rendered moot by the mere fact that parental care is adaptive.

We conclude UO by saying that the case against evolutionary altruism has already collapsed when judged by normal scientific criteria. The case against psychological altruism has not yet collapsed (as we cheerfully admit), but the cracks are so large that one is well-advised to stand clear. Trivers may regard these edifices as his home, which may explain his anger and denial. Others may rejoice, although Trivers is right that multilevel selection has its dark side. We think that UO has achieved a kind of scientific pluralism that allows nature and human nature to be viewed more clearly, warts and all. Readers of SKEPTIC, with their penchant for challenging conventional wisdom, should read UO, return to Trivers’ review, and judge for themselves.

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REVIEWS OF *UNTO OTHERS*

In the interest of objectivity, excerpts of all reviews are provided, including some that are highly critical. The polarized nature of the reviews suggest that fundamental issues are at stake.

John Maynard Smith, *Nature*, June 18: “This book should come with a health warning. Read critically, it will stimulate thought about important questions. Swallowed whole, its effects would be disastrous.”

Iver Myrsterud, *Trends in Ecology and Evolution*, November 11: “*Unto Others* is one of the most important books of the decade. It simply cannot be ignored, as it is the most comprehensive treatment of the whole levels-of-selection debate, including its history, so far. *Unto Others* will inspire a flood of new studies, invite debate and be at the center of intellectual discourse for the next decade. We live in an exciting time, and I look forward to seeing what comes out of the process from this ‘must’ of a synthesizing book.”

Len Nunney, *Science*, September 11: “This book is more focused on debate than science... Anyone looking for novel scientific insight will be sadly disappointed.”

Richard Lewontin, *New York Review of Books*, October 22: “Intellectual work is supposed to be a combination of originality and hard thinking. Unfortunately, there is some contradiction between these, at least in evolutionary theory. Careers are often made either from an ambitious but poorly thought out originality, or a skillful but mechanical analysis of a well-worn theme. *Unto Others* is precisely that combination of radical reexamination of a system of explanation, an examination from the roots, with a rigorous technical analy-

sis of both biological and epistemological questions that we are all supposed to engage in.”

Laurence Hurst, *New Scientist*, September 12: “For one thing, Sober and Wilson’s language is a recipe for confusion...The present linguistic concentration on individual-level selection has created a scientific culture in which it is normal to hypothesize about how various features of organisms (eyes, wings and so on) might be “good for the organism.” Sober and Wilson wish to create a culture in which it is normal to hypothesize about how features might be “good for the group.”

Philip Kitcher, *London Review of Books*, October 15: “For two decades, Sober, an internationally prominent philosopher of biology, has provided welcome clarification of the concept of natural selection, while, for an even longer period, Wilson, a well-known theoretical biologist, has campaigned to rehabilitate one of the most vilified views about the nature of selection...Defenders of psychological altruism can no longer be indicted on the grounds of wishful thinking.”

Kenneth Binmore, *Managerial and Decision Economics*, in press: “This stylishly written and thoughtful book seeks to answer two large questions: How can altruism be compatible with evolution? To what extent are people genuinely altruistic?...I recommend this book strongly to those who appreciate that we need to understand what evolution has made of human nature before we can learn to harness our capacity for unselfish behavior on the large scale necessary in a modern industrial society. In spite of its occasional failure to turn the other cheek, I think it may well

sound the final knell of the group selection controversy.”

Paul Rubin, *Bioeconomics*, in press: “Among many evolutionary biologists, it is a matter of faith that group selection, while theoretically possible, in fact is so improbable as to not be worth mentioning. This book is a challenge to that belief. To economists interested in evolution, the book is essential...The issues raised are of profound importance for economists interested in behavior of humans in group settings, which is where all economic behavior occurs.”

Chris Boehm, *American Anthropologist*, in press: “Now, a major paradigm adjustment could be in the making—one that will affect the way we think about humans as social animals. By boldly expanding the ultimate basis for explaining social behavior, *Unto Others* could be extremely useful in restoring some of our broader anthropological interests in evolutionary issues. It also serves as an important model for how methodological individualism and methodological collectivism can be effectively combined. I believe that a close reading of *Unto Others*...could help anthropology re-integrate itself...*Unto Others* opens up important new possibilities that we cannot afford to ignore.”

Kim Sterelny, *Biology and Philosophy*, in press: “*Unto Others* is a fine book. It is a clear, cogent, and in places entertaining, defense of an important picture of evolution in general and human evolution in particular... I think they are right to think that group selection has been of especial importance in human evolution. Furthermore, their psychological speculations are plausible. Indeed, they give egoism and hedonism more airtime than they deserve.”

THINK FOR YOURSELF

TRIVERS REPLIES TO SOBER AND WILSON

FIRST THINGS FIRST. I freely admit to having written an incomplete review. A second paragraph should have been included giving a thumb-nail sketch of the content of the book. Numerous people have drawn my attention to this omission. It is a disservice to the reader (and to the authors) and I apologize to both. I am also guilty of overemphasizing the degree to which Sober and Wilson seem not to see group selection’s ugly co-twin. They do see it, they conceptualize it correctly and they devote a few pages to its description. It would have been better if I had said that I believe they did not give the subject nearly the attention that logic suggests it deserves.

Wilson and Sober use language carelessly in their very first sentence (and then throughout their response). In 1964, Hamilton defined the terms under discussion: a *selfish trait* is one that confers a benefit on the actor while inflicting harm on another individual (not the child of the first) where harm and benefit are measured in terms of effects on reproductive success (number of surviving offspring), and *altruistic behavior* is the reverse. Selfish behavior is expected under classical natural selection, altruistic behavior is not. Hamilton then showed that genetic relatedness could generate selection for

altruistic behavior, as defined, and I showed in 1971 that a kind of altruistic trait could evolve if there were a series of interactions between two individuals where benefits and costs could often be reversed so that reciprocal relations could be favored by natural selection. I naively thought that Hamilton and myself had, thus, demonstrated two conditions under which altruistic traits could be favored by natural selection. Yet Wilson and Sober’s use of language suggests exactly the opposite. Apparently we demonstrated that life is more deeply selfish than we had imagined. This is a perverse use of language, equating “selfish” with “self-promoting” or “self-benefitting.” We do not say of someone who loves his children, helps his family and friends and treats his neighbors with respect, “What a selfish brute he is,” yet all of these traits may be genetically self-benefitting. Toward the end of their comments, they use “selfishness” to refer both to intragenomic conflict and genes beneficial at the level of individuals. Both count as examples of “so-called ‘individual selfishness’ as far as Trivers is concerned” but this really is adding insult to injury, a case of projecting their own verbal slovenliness onto me, because I have made a conscious effort in my work to avoid the verbal confusion

they promote. In my textbook, for example (*Social Evolution*, 1985) I use “selfish genes” only to refer to genes that promote their own rate of transmission or a minority kinship outlook, i.e. instances of genes beneficial to themselves but costly to the majority of the other genes in the same individual!

Wilson and Sober’s reply, like the book itself, has an unusually high ratio of personal, biographical and imaginary information compared to information that bears on the logic or the facts of the matter allegedly under discussion. Coconuts knock, an absurd fantasy about U.S. history is indulged, Tonto and the Lone Ranger make a full appearance, G.C. Williams and W.D. Hamilton are once again dragged out of hiding to give their group selection testimonials, and my own psyche is laid bare. Although I am said to invoke the “authority” of Hamilton and Williams’ work, I try to invoke the authority of no one (but, of course, to borrow any logic that seems appearing). I do not care whether at their annual convention 900 howling group selectionists endorse *Unto Others* in its entirety or whether the only true believers are a deeply repentant W.D. Hamilton and a devout monk lost somewhere in the Himalayas. I want to understand the matter for myself.

Wilson and Sober tell us that coefficient of relatedness (r) does not disappear from the Price equation but instead becomes “more generally,” “a degree of correlation between the genotype of the individual and the average genetic composition of its group.” And that is exactly the point. We have left the clear, simple world of genetic identity-by-descent and variation in r ; we must now think in terms of a correlation with the average genetic composition of a group. This is similar to a mistake Haldane made in the 1950s. After giving the kinship argument correctly, he then (for other reasons) rejected the possibility of individual behavior being adjusted to individual r ’s and imagined that selection only acted on the average r to group members, thus eviscerating most of the theory. Furthermore, there are several processes that can cause genetic correlation, kinship being only one, but kinship is distinguished by little, or only modest, within-genotype conflict over actions toward others, while other means of assortment usually pit a small, correlated part of the genome against a much larger, non-shared portion.

Wilson and Sober argue that by merely partitioning selection into its components they have demonstrated that between-group selection is an important evolutionary force! This is typical of their penchant for verbalistic advances instead of real ones. You also have to demonstrate the power of each component, preferably under well-defined conditions. Watch out for these people. They will sink a series of verbal distinctions until almost everything is a form of group selection, flap their wings a couple of times and suddenly we are talking about ecosystems as super-organisms. A little bit more argumentation along the way would be helpful.

Wilson and Sober raise an interesting point when they ask how 5% selection pressures at the level of individuals can suppress intragenomic pressures of 50%. That the latter often reach 50% is all but cer-

tain. Meiotic drive, B chromosomes and systems of paternal genome loss, for example, usually involve nearly complete drive in one sex and none in the other, for an average effect of almost 50%. Of course, there are exceptions. There is also no doubt that under extreme conditions (i.e. very high frequency of the driving element), selfish genes can generate 50% selection pressures at the level of the individual, e.g. through the deleterious effects of homozygous drivers. It is an empirical fact that such frequencies are very rare in nature, the mean frequency typically below 10% and hence causing weak selection pressures at the level of individuals. The conventional answer to the question Wilson and Sober raise is that the weak selection pressures act on a huge number of genes (all those unlinked to the driving haplotype itself) so that you are pitting about 1% of the genotype against 99%. It is not at all clear what the analogy of this is to group versus individual selection. Unlike genes within genomes, individuals within groups do not spend their lives locked within an unchanging assemblage of individuals, all of whom live or die together, their only escape being via reproduction. Is the best analogy at the group level the tendency to hire a police force to deter egregiously selfish behavior?

I want to imagine a third visitor to my office, this time a woman eager to learn about the new group selection. I would tell her, by all means, start with *Unto Others* but try to move quickly beyond it. For example, if after a moment’s reflection, you agree as I do, with Wilson and Sober’s condensation of the second half of their book—namely, that group selected mechanisms could be psychologically selfish and vice-versa—then I think you can safely skip this half. If variances and co-variances give you a headache, as they do me, consider working in another area of biology. If not, master the Price equations, their use in sex ratio theory and study where else they have been applied. Pay close attention to between-group migration or dispersal and its effects on intensity of selection. Be sure you know at each moment what you mean by a group. Skip the philosophy, pay little attention to the “history” of group selection and try to get down to cases. Wilson and Sober tell us that kinship theory and reciprocal altruism are special cases of group selection, so study them in their own right and see if you can dream up other special cases, but be sure to keep kinship, reciprocal benefits and some, general group benefit separate in your mind. Again, get down to cases. Whether warfare or the spread of a religious cult or competition between corporate-like entities, get specific and try to model the matter in detail. See what kinds of group selection process best explains the available evidence. If interested in psychology, go right to the work that shows that all you have to do is to divide humans into groups—it can be quite arbitrary, strangers into a blue-shirted team and a yellow-shirted team—and you seem automatically to engender processes of group identification and group-level glorification and self-deception. Finally, do not waste much time with book reviews, counter-arguments to same and whether the rest of the world is on board or not. Think the thing through for yourself.

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