BOOK REVIEWS

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EVOLUTIONARY BIOLOGY AND HUMAN ALTRUISM: A REVIEW OF THREE BOOKS

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In *Unto Others*,[2] Elliott Sober, a noted philosopher of evolutionary biology, and David Sloan Wilson, a lifelong student of group selection, argue from evolutionary theory, philosophy, and psychology that, despite today's nearly exclusive preoccupation with self-interest, ultimately altruistic motives also influence human action. In *The Origins of Virtue*,[3] originally published in 1996 and recently republished by Penguin, the science writer Matt Ridley likewise argues that natural selection favors trust and virtue in some human relationships. In sum, both books argue that prehistoric humans depended on fellow tribe members for survival in warfare with other tribes, and that pure egoism is utterly inconsistent with the fellowship and trust required for this interdependence. The challenges these books pose to the economists' (and many evolutionists') view that humans are egoistic animals whose only motive is self-interest are important and timely. Are their arguments sufficient to dethrone Madison Avenue's dogma?

Some doubt whether any argument from evolution could do so. In *The Temptations of Evolutionary Ethics*,[4] recently republished in paperback, Paul Lawrence Farber, a historian of science, reviews the history of attempts to apply evolutionary biology to ethics. He finds that, so far, this history is one of failure without end. Ventures in evolutionary ethics fall into two general classes. The first seeks to demonstrate that ''those mental and moral qualities most peculiar to mankind (are) analogous, in their nature, to the mental and moral qualities of animals'' (Fisher 1958, p. 189), thus bringing the evolution of morality within the purview of natural selection. Thus Darwin (1871, p. 166) argued that, for most of human prehistory, selection among groups of human beings favored altruism among the members of a group:

> . . . although a high standard of morality gives but a slight or no advantage to each individual man and his children over the other men of the same tribe, yet . . . advancement in the standard of morality . . . will certainly give an advantage to one tribe over another. There can be no doubt that a tribe including many members who . . . were always ready to give aid to each other and to sacrifice themselves for the common good, would be victorious over most other tribes; and this would be natural selection.

More frequently, evolutionary biology is used to justify ethical convictions acquired from other sources: Farber cites Herbert Spencer and Julian Huxley as familiar examplars of this approach.

Farber notes that there have always been biologists, such as T. H. Huxley in the 19th century and George Williams in our own, who see no trace of morality in the animal world. Such biologists are as opposed to evolutionary ethics as the most conservative of those theologians who are ever seeking to deepen the moat between human beings and other animals. Similarly, few philosophers have found evolutionary biology a suitable foundation for ethical systems. Farber (p. 175) himself dislikes supposedly universal ethical systems. For him, a central lesson of evolutionary ethics is how readily we project our own values on nature. Can Sober and Wilson, or Ridley, overcome these criticisms?

David Hume's remark that one cannot deduce what ought to be from what is seems to exclude an ''evolutionary ethics.'' Yet, as Hume himself recognized (Farber, p. 159), knowing what is helps us achieve what ought to be. Many knew this long before Hume. For example, Aristotle knew that children **should** be cared for. In his *Politics* (Book II, chapter 3), he remarked that we have families because, if children were shared in common, a boy, being everybody's son, would be neglected as if he were nobody's, because no **one** would be responsible for him (Barnes 1984, p. 2002). Plato believed that a city's welfare depends on harmonious cooperation among its citizens. Accordingly, in the *Republic* (Book I), Socrates's first convincing argument for justice centers on the two questions: ''Do you think that a city, an army, or bandits, or thieves, or any other group that attempted any action in common, could accomplish anything if they wronged one another?'' and ''If it is the (property) of injustice to engender hatred wherever it is found, will it not, when it springs up either among free men or slaves, cause them to hate and be at strife with one another, and make them incapable of effective action in common?'' (Hamilton and Cairns 1961, p. 602).

Evolutionary biology sheds little light on the ultimate goals of ethics. Yet many voices tell us that we must understand its analysis of ''what is'' in order to attain these goals. We are told that natural selection has given us an ''animal nature'' of utter egoism (never mind that this egoism is most

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[2] *Unto Others: The Evolution and Psychology of Unselfish Behavior*. Elliott Sober and David Sloan Wilson. 1998. Harvard University Press, Cambridge, Massachusetts. 416 pp. HB $17.95, ISBN 0-674-93047-9.

[3] *The Origins of Virtue: Human Instincts and the Evolution of Cooperation*. Matt Ridley. 1998. Penguin, New York. viii + 295 pp. PB $13.95, ISBN 0-14-026445-0.

[4] *The Temptations of Evolutionary Ethics*. 1994. Paul Lawrence Farber. University of California Press, Berkeley, California. xii + 210 pp. HB $45.00, ISBN 0-520-08773-9; PB $16.95, ISBN 0-520-21369-6.

evident where civilization has done its worst), and that morality must defend civilization against this egoism. Those whose self-appointed mission is to keep us in the ''real world'' by harping on phenomena once blamed on the ''prince of this world'' (never mentioning those that make us rejoice in the beauty of nature or the experience of friendship), relentlessly emphasize this egoism. Sober and Wilson try to redress this imbalance by showing that altruism, as well as egoism, is an essential part of human nature. Ridley, who rather prides himself on his lack of illusions about Satan's princedom, nonetheless seeks to demonstrate the evolutionary roots of trust and virtue. They go about it in very different ways.

Sober and Wilson argue that past selection among human groups has created a degree of altruism among human beings. The first half of their book is one long argument for the crucial importance in evolution of selection among groups. This argument is evangelistic. There are occasional refusals to understand the motives or merits of competing viewpoints. Sometimes the concept of group selection is stretched to include phenomena most people find easier to understand in other terms. Do these faults destroy their argument?

There is reason for Sober and Wilson's evangelism. Many people, both in biology and on its fringes, think that selection among groups is nearly irrelevant to evolution. Commenting on ascribing altruism to selection among human groups, Farber (p. 163) remarks that ''Group selection, however, is accepted by few scientists today.'' Similarly, Ridley (p. 175) proclaims that ''biologists have undermined the whole logic of group selection.'' Indeed, something more than just skepticism is sometimes involved in the rejection of group selection. Citing George Williams, Ridley (p. 193) asserts that ''preferring the morality of group selection to the ruthlessness of individual struggle is to prefer genocide over murder.''

Sober and Wilson see group selection wherever Price's (1972) two-level version of Fisher's (1958) fundamental theorem of natural selection is applicable, that is to say, in any population that can be partitioned into subgroups, variation among which influences how allele frequencies change in the population as a whole. These subgroups need not be ''units of heredity;'' indeed, they usually are not. As Price's formalism applies to any population where an adult's reproduction is limited by interactions with a few permanent neighbors, while young disperse far beyond this neighborhood, Sober and Wilson think group selection is well-nigh ubiquitous.

Much that Sober and Wilson call group selection, however, others call by different names. George Williams (1966, pp. 22–24) recognized genes, but not sexually produced genotypes or phenotypes, as fundamental units of selection, because only genes are inherited intact. Individuals are adapted only because the common interest of the genome in fair meiosis ensures that selection favors only those alleles which benefit their carriers (Leigh 1991). On the other hand, groups that exchange no migrants and ''reproduce'' by one group splitting into two, can be viewed as units of heredity and, therefore, of selection. Such selection among groups transformed quondam parasites into indispensable mitochondria, each group being one cell's protomitochondria (Leigh 1983). The view that group selection occurs only when groups are distinct enough to be units of heredity is reflected in the widespread agreement that group selection is effective only if migration among groups is minimal, groups are shortlived, and group reproduction is uniparental (cf. Hamilton 1975, Ridley, pp. 179, 186).

Argument over how best to apply names to things is most acute for how ''local mate competition'' (Hamilton 1967) affects sex ratio. Consider the appropriate ratio of sons to daughters for parasitoid wasps laying eggs in a fly pupa. One or more fertilized female ''foundresses'' lay eggs in the pupa; the larvae grow, metamorphose, and mate among themselves (competition for mates is local because males compete only with other sons of the few parasitoids laying eggs in their host pupa). Then fertilized females leave to search for other pupae. The optimum ratio of sons to daughters for these parasitoids is most easily found by using Price's (1972) theorem to analyze the balance between selection within a pupa for a 50:50 sex ratio, which maximizes the proportion of a foundress's genes among those exported from her pupa and the differential contribution of genes to future wasp generations from pupae with more female-biased sex ratios. To Sober and Wilson, as to Colwell (1981), the higher output of fertilized females from pupae with more female-biased sex ratios is group selection. Charlesworth and Toro (1982) countered that local mate competition favors a female-biased sex ratio even if individuals are uniformly distributed, as long as competition to fertilize a female is limited to a few nearby males, and fertilized females disperse far beyond this neighborhood. Why call local mate competition group selection when it has the same effect in the absence of discrete groups?

Sometimes, Sober and Wilson stretch group selection beyond its natural limits. On p. 94 kin selection is viewed as a form of group selection, each group being the relatives with which an individual interacts. As with local mate competition in continuously distributed populations, the ''groups'' centered on nearby individuals overlap without coinciding: for Sober and Wilson, these processes are still group selection. On p. 96, Sober and Wilson say that, where selection on different characteristics of an individual is shaped by interactions with different sets of neighbors, each set represents a group relevant to a particular group selection.

With rigid logic, Sober and Wilson insist that what drives selection among individuals is **relative** fitness. Therefore, when several must cooperate to bring an overloaded dinghy safely to shore, they ascribe a shirker on that boat an advantage over his working companions, even though this ''advantage'' opposes his self-interest if all drown unless all help. After all, if shirking drowns the shirker, he benefits by cooperating. When discussing selection for suppression of ''segregation-distorter alleles,'' which spread a phenotypic defect through a population by biasing meiosis in their own favor, Sober and Wilson again invoke group selection in defiance of common sense. They say that a mutant at an unlinked locus which suppresses the distortion, that is, restores the fairness of meiosis, is spread by group selection because the suppression must involve some cost to the mutant, whereas the whole genome benefits from fair meiosis. Nevertheless, the greater freedom of the mutant's descendants from the distorter's phenotypic defect (thanks to the arrested spread of the distorter's defect among them) com-

pared to their wild-type counterparts is what drives the mutant's spread. For the population geneticist, this is the one crucial comparison. Is it not better to say that, because mutants restoring the fairness of meiosis are favored at every locus not linked to the distorter, fair meiosis serves the common interest of the whole genome?

Group selection is not always the best framework for analyzing mutualism. At bottom, interdependence among the members of a human group is what calls forth the evolution of altruism. Because members of a group depend on each other, they share a common interest in cooperating. The language of common interest, more readily than Sober and Wilson's, leads one to ask when an individual benefits by cheating his fellow group members, that is, when the interest in cooperating ceases to be common to all. More generally, just what factors create a truly common interest? Need it be enforced, and if so, how?

None of these criticisms affect Sober and Wilson's argument for human altruism: some even suggest how this argument might be strengthened. Sober and Wilson speak of real processes, whatever one may choose to call them. Sober and Wilson's odd use of the group selection concept is no excuse for those who reject the possibility of genuinely altruistic motives to disregard their book.

Indeed, there is much to learn from Sober and Wilson's book. Price's (1972) theorem suggests that the group's good prevails over individual advantage, either if the phenotype under selection influences the fate of groups disproportionately more than the advantage of individuals or if heritable variation among groups exceeds the product of heritable variance within groups and average group lifetime as measured in individual generations (Leigh 1983).

Individual advantage can be related to the good of the group in unexpected ways. In many nonlinear predator-prey models, an improvement in predator efficiency that slightly decreases the abundance of prey required to maintain the predator's numbers could destabilize the relationship, causing the predator population to oscillate to extinction. Gilpin (1975) constructed a plausible model where selection among groups of predators and their prey favored predators sufficiently prudent to avoid extinction. This group selection was driven by the disproportion between the danger of extinction and the slight individual advantage of greater efficiency. Sober and Wilson (p. 122) tell an even more sobering story about selection for egg production in hens. Selection of hens laying the most eggs proved counterproductive, for in the crowded conditions of industrial chicken farms, these hens mauled their neighbors, reducing their group's egg production. In contrast, selection for **groups** with the highest total egg production, modeled on Michael Wade's experiment with group selection on flour beetles, proved as useful as selecting the most productive hens was futile. Here, selection for productive groups favored lower aggressiveness among the hens, reducing mutual injury.

Concerning the ratio of variance among to variance within groups, one thing new to me (although well known to theorists of cultural evolution) is how group-specific social norms can enhance the effectiveness of selection among groups by diminishing within-group variance. Sober and Wilson review evidence for the almost aggressive egalitarianism of ''small-scale'' societies, especially hunter-gatherers. In these societies, social norms enjoin sharing of windfalls and mutual assistance to counter both individual misfortune and communal crisis and constrain excess ''private'' accumulation and claims to power and influence. Such norms reduce tensions within a group and make it more effective. By diminishing inequality, these norms also tend to equalize opportunities for reproduction, diminishing within-group variance and making selection among groups more effective. Are such ''equalizing'' norms the norm? Unusually for books of this type, Sober and Wilson do not rely exclusively on anecdote: to find out, they sample 25 societies at random from the Human Relations Area File, taking the first 10 pages about social norms from the report on each sampled society. The preliminary conclusions from a test which is still being refined is that, in most societies, behavior is tightly regulated, though far from completely controlled, by social norms. Some norms enjoin mutual assistance and sharing of resources, others suppress inequality in power.

Are genes involved in this cultural group selection? Extensive migration among groups will not subvert this process, if immigrants absorb the cultural norms of their new group. Social groups use various means to ensure the inculcation of their norms among those joining. The Hebrew Torah, for example, outlawed marrying a woman from a nearby Canaanite group (who might have neighbors to remind her of her own norms), although a wife from a more distant society was acceptable, provided she accepted the norms of the Torah. The relationship between genes and social behavior can be as weak in animals. Smythe (1991) created a strain of social pacas from fiercely territorial parents by raising the first generation under special conditions and placing them in a common cage: social traditions persisted among their descendants in this cage with no further interference from the investigator.

Sober and Wilson conclude their case for group selection among human societies by providing an example where a stronger ethic of mutual assistance is enabling one African society to replace and/or absorb another.

The second half of this book discusses philosophical arguments concerning human altruism and psychological experiments testing whether human motives are ultimately entirely egoistic. This section of the book is much less contentious in tone and seems scrupulously fair. Its two lessons are how easy it is to find fault with a philosophical argument (a lesson particularly effective when, as happens here, the arguments involved support the authors' position) and how difficult it is to decide what would constitute decisive evidence for an ultimately altruistic motive. Some might find this difficulty surprising. Isn't this question settled by the nearly universal conviction that anyone can distinguish the truly generous from those who help in hope of future reward? Our fury at being let down by someone we have helped might suggest egoism, but Adam Smith observed that many are angered when someone else is let down thus. Is the presence of genuinely altruistic motives in human beings one of the propositions Pascal says we can know to be true but never prove?

Sober and Wilson try to circumvent this conundrum by saying, in essence, that ultimately altruistic motives must

have evolved because, over most of their evolutionary history, human beings survived by helping fellow group members on whom their own survival depended. Sober and Wilson argue that, just as what an animal knows about its environment, it should know truly in order to behave appropriately (cf. Lorenz 1977), so the interdependence of fellow group members requires cooperation motivated by genuine altruism, not just help rendered from calculated self-interest. This is reasonable **if** truly altruistic instincts are available for selection.

Ridley's discussion of the evolution of trust and virtue anticipates Sober and Wilson in many ways. They develop many of the same examples. Like Sober and Wilson, Ridley concludes that humans have instincts favoring altruism and morality because, in the past, these features were crucial to the survival of groups whose members' very lives depended on close cooperation with their fellows. Ridley's book differs from Sober and Wilson's, however, in two major ways.

First, Ridley is given to an ''adaptive storytelling'' that sometimes runs wild. He seems to have learned nothing from the fiasco of the vulgar human sociobiology of the 1970's. An egregious example of this ''storytelling'' is Ridley's (pp. 186–193) indiscriminate ascription of a whole suite of social manifestations of human sinfulness to an instinctive tribalism that defines one's identity by irrationally antagonistic contrasts with members of other tribes. His book has many merits; it is a pity to see it marred by this kind of loose talk.

Second, Ridley founds his argument on Dawkins's assertion that a characteristic spreads only if it serves the interest, that is, increases the frequency, of some gene; he explicitly rejects group selection. Because the genes of a genome depend on each other, natural selection is most likely to favor characteristics which serve the common interest of the genome programming it.

Ridley focuses on how mutualisms evolve and are preserved. He treats the usual topics: the mutual benefits of division of labor; the strategies which best enforce cooperation in the ''iterated prisoner's dilemma'' game, where two players achieve maximum sustained output by cooperating at each play, although cheating yields more profit on any one play; how interdependence among members of a human group promotes trust and virtue among them; how social norms and cultural evolution help to promote these moral qualities, and the like.

The rhetoric of ''selfish gene theory'' can be remarkably silly. Ridley (p. 19) reports Hamilton's (1996, pp. 133–134) blame of his own indecisiveness on the conflicts of different groups of genes in his genome—as if our genes are what express our consciousness and will! After all, our selfish genes survived by programming fully functional individuals. This sort of reductionist non sequitur has a curiously wide appeal. The freedom of human wills and the validity of spiritual experience are often denied in the name of a physical determinism that cannot possibly be demonstrated precisely enough to justify such conclusions, a determinism extrapolated from phenomena ever so much more remote from human experience than those denied in its name.

Selfish gene rhetoric imposes an unsettling oscillation on Ridley's book. One chapter rings the changes on tribalism and intertribal hatred, the next shows how trade promotes conviviality among members of different tribes. One chapter proclaims that prehistoric people cared no more for the environment than we do because they exterminated the ''megafauna'' of so many lands. The next shows that indigenous societies are effective conservators of those resources they can defend against outsiders.

Ridley also takes a snide pleasure in destroying what he views as romantic illusions. Some babies are thrown out with the bathwater. He denies the relationship between Adam Smith's *Theory of Moral Sentiments* and his *Wealth of Nations,* not seeing that competition among individuals serves the common good only if, as outlined in *The Theory of Moral Sentiments,* members of a community have the will and the power to discern and enforce rules of fair competition. He never comes to a just assessment of the relationship between primitive peoples and their environments, because he remembers the negative aspects more clearly than the positive.

On the other hand, selfish gene theory makes Ridley focus on those aspects of mutualisms which discourage or prevent freeloaders, a focus which is absolutely crucial to understanding how mutualisms evolve. Ridley also recognizes the crucial point that altruism is a facultative, condition-dependent response. Ridley tells how opening a commons to all users by government fiat leads to its destruction, by denying local villagers the profits of preserving it. Indeed, Ridley is no friend of big, unresponsive government. He is less explicitly sensitive to the disruptive powers of multinationals (maybe he blames them on Big Government?). Neither book mentions how altruistic instincts might be affected by the destabilization of neighborhoods so characteristic of modern society, which demands that people move where the money is.

The contrast between Ridley's mode of explanation and Sober and Wilson's is perhaps best revealed on Ridley's p. 188:

> Most of the examples I have discussed are cases where individuals are cooperating to further their self-interest. That is not group selection: it is individual selection mediated by groupishness. Group selection occurs when individuals cooperate against their own self-interest but in the interest of the group. . . .

Just as Sober and Wilson justify invoking group selection by splitting hairs in such a way that any cooperation must be disadvantageous to the cooperator, so Ridley's gut dislike of group selection leads him to claim that, to be genuine, group selection must oppose the self-interest of the individuals involved. Curiously, Ridley readily invokes individual selection with no thought of infringing genic self-interest. Elsewhere, Ridley views group selection as selection among entities distinct enough to be units of heredity, and assumes that all other cooperation reflects mutual self-interest, an idea Sober and Wilson appear to consider self-contradictory.

Where have Sober and Wilson, or Ridley, got us? I don't think they offer any ethical lessons that one could not obtain from a careful and judicious reading of Aristotle's *Politics*: to wit, that thanks to our interdependence, we must hang together or hang separately, and the best way to hang together is to treat each other as we wish to be treated. These books do help counter the myth that our heritage from natural se-

lection is one of unmitigated egoism, Sober and Wilson more effectively than Ridley, who sometimes allows his selfish genes too much personality. Frans de Waal (1996) has triumphantly vindicated the thesis of these books by demonstrating that chimpanzees have a rudimentary sense of justice, in that they instinctively recognize what behavior serves their group's common good; they remember and repay favors; and they do retaliate against those that won't repay.

Both Ridley and Sober and Wilson tell the story of how taking astronomy does not change the proportion of students likely to engage in mild altruism, whereas taking freshman economics, which preaches the supposedly rational egoism of economic man, drastically lowers this proportion. Is our morality shaped primarily by our defining myths? If so, it is time to dispel the demonstrably erroneous myth that natural selection has left us a purely egoistic nature.

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