

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.

Group selection and "the pious gene"

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Abstract: If selection at the group level is to be considered more than a mere possibility, it is important to find phenomena that are best explained at this level of selection. I argue that human religious phenomena provide evidence for the selection of a "pious gene" at the group level, which results in a human tendency to believe in a transcendental reality that encourages behavioral conformity to collective as opposed to individual interest.

For social psychologists like myself, one of the most exciting aspects of the advances in evolutionary theorizing over the past twenty years has been the development of our ability to make sense of human social phenomena by looking at their counterparts in other animals and comparing the evolution of these alternative social forms of life to hypothetical accounts of the evolution and functions of our own social capacities and activities. The result has been a more integrated understanding of human nature.

Until now, most of these advances have been made while maintaining a strict theoretical individualism. The individual could be viewed as a fitness optimizer who uses social means to pursue individual (or at most inclusive) fitness ends. However, religious phenomena have always been a source of embarrassment for this pursuit of a strict individualism. Thus, it is interesting to note that E. O. Wilson (1978) willingly endorsed a group-selection strategy to account for these phenomena. Now, D. S. Wilson & E. Sober (W&S) (1994) have provided us with a general defence of the use of group selection as a theoretical strategy through an adaptation of Dawkins's concept of "vehicle" and have illustrated their framework on a particular case of religiously based group phenomena – the Hutterites (see sect. 2.6).

I wholly endorse W&S's attempt to bring a more rigorous group-selection approach to theorizing about human evolutionary biology. I was also pleased to see that a number of commentators on the target article not only accepted the vehicular approach but also made concrete suggestions on how to turn the – almost taboo – concept of group-selection into one more tool we can bring to bear on social phenomena in a variety of biological species, including humans (e.g., Miller 1994). It seems to me, however, that with the exception of MacDonald's (1994) commentary on competition between ethnic groups, there have been no serious attempts to show how group selection might operate in human societies. This is unfortunate, because one of the major criticisms

of the target article was that group selection, although conceptually possible, so rarely occurs that it is of minor importance (e.g., Moore 1994; Nesse 1994; Simpson 1994). I will try to show how the vehicle concept of group selection might help us develop a general understanding of religious phenomena.

There are a variety of religious phenomena which have no obvious individual fitness value on their own, but which seem to support the individual's identification with a group of coactors who might gain some collective advantage from coordinated activity. Could such religious phenomena and collective activity have emerged through the selection of a "pious gene" (Matson 1993), the group serving as the primary vehicle of selection? Mol (1976) has defined religion as the "sacralization of identity" and has suggested that it is chiefly exhibited through four interrelated mechanisms: (1) *objectification*, whereby mundane existence is ordered within a timeless transcendental reality, (2) *commitment*, which involves an emotional attachment to the group identity, sometimes mediated through charismatic individuals, (3) *ritual*, which includes activities that rehearse and reinforce the objective transcendental reality and group identification, and (4) *myth*, which provides a narrative ordering and structure to this transcendental realm. Simply put, it is difficult to see why individual self-interest agents should expend so much energy to construct and reaffirm a transcendental reality which at best correlates only partially with the pragmatic truths of mundane existence. Why do we expend so much energy supporting the transcendental realm of what Matson (1993) calls "high beliefs" that are neither confirmable nor disconfirmable, in addition to mere "low beliefs," which are pragmatic and testable? Has a "pious gene" evolved, inclining humans to generate and support such high beliefs and the religious activities associated with them? And, if so, what is the function of these beliefs, if they have no direct pragmatic fitness value?

The obvious answer to these questions is that high beliefs and transcendental realities serve to coordinate group activity, (1) internally in terms of norms, rules, roles, statuses, and collective activities, but also (2) externally in direct as well as indirect competition with other groups, and (3) ecologically, with respect to factors limiting the carrying capacity of the environment (see, e.g., Campbell 1975; 1991; Durkheim 1915; Harris 1979; Matson 1993; Mol 1976; Rappaport 1971; Wilson 1978). Selective processes involving religious phenomena operate at a group level of selection and produce net fitness gains for individuals who are members of particular religious groups, despite sometimes being opposed by selective processes that operate at the individual level. Moreover, it seems that a refined understanding of the roles of

individual and group vehicles in selection will help us see just how the psychological processes associated with religious activities might have evolved.

I will close by considering in some detail a hypothesis about one of these psychological processes that has its roots in Bergson (1935) but has recently been used by Simon (1990) in a quantitative model of selection. Bergson's idea was that morality and religion emerged as phenomena which substitute for absent instincts in human nature. Because of the evolution of intelligence and rationality in conjunction with relatively weak instincts, humans are capable of a wide range of alternative behaviors. This would produce chaos in social groups if it were not opposed by a counteracting force. So an alternative instinct was selected for in our irrational deference to authority, especially moral and religious authority that is grounded in a mythological realm of "illusory perception" and "a counterfit of recollection." Bergson saw this transcendental realm of religious belief as "a defensive reaction of nature against the dissolving power of intelligence" (p. 122). It served to support the functioning and preservation of the social group by providing authoritative truths to oppose to the pragmatic truths that it is human intelligence's special province to acquire and to the tendency of individuals to pursue egoist interests based on these pragmatic truths.

Simon (1990) refers to our "docility" in social learning from authoritative sources. Furthermore, using a variation of the mathematical model of group-selection described in the target article, he postulates that a gene for docility, because it causes sufficient advantages to be gained from the practical aspects of sociocultural knowledge (i.e., low beliefs) could also cause the transmission to individuals of altruistic behaviors which might even be against their individual self-interest (i.e., high beliefs). Because human rational knowledge is bounded, we must often act in situations where the consequences of our actions for self-interest cannot be rationally cognized. If, in such circumstances, social knowledge is likely to yield a net gain for the docility (or may we suggest "pious") gene, which may be due, in part, to the transmission of behavioral strategies that are adaptive only if held uniformly at the group level, then it will be selected for, even if it is sometimes opposed by more individualistically selected psychological mechanisms. It seems that religious phenomena epitomize just those situations where this conflict of mechanisms is most intense. In such circumstances docility toward sacred high beliefs of an absolute authoritative nature can cause the more individualistic intellectual processes to forfeit their usual self-interested authority over action, while often providing a net return to the members of groups who accept this sacred authority.

Varieties of group selection

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Abstract: Group selection may be defined either broadly or narrowly. Narrowly defined group selection may involve either selection for altruism or group selection between alternative evolutionarily stable states. The last variety of group selection is likely to have been particularly important in human evolution.

Much of the argument over group selection (Wilson & Sober 1994) (W&S) comes from the fact that different parties have different definitions and models of group selection. I think it is useful to distinguish between group selection broadly defined and group selection narrowly defined, and, within the latter category, between group selection for altruism and group selection between alternative evolutionarily stable states.

1. Group selection broadly defined. Imagine a population of farmers subdivided into a large number of groups. Farmers' fields

are raided by voles. Most farmers don't do anything about the voles, but Fred the mutant farmer goes out and kills voles. Suppose that (1) there is a cost, C , to killing voles, which is borne by Fred alone; (2) there is a benefit, B , to killing voles, gained by all the farmers in Fred's group, since voles raid the fields of everybody in the group. If B is greater than C , then Fred will be worse off than other members of his group, but better off than the average farmer (averaging over all groups). In other words, there is a within-group component to Fred's fitness, which is negative, and a between-group component, which is positive. Fred's overall fitness is positive, and the vole-killer mutation will spread. This is a case of group selection broadly defined (GSB). For a trait to be favored by GSB, there must be a within-group and a between-group component to individual fitness, and the latter must be greater than the former. Kin selection and local mate competition à la Hamilton are instances of GSB. W&S treat GSB as group selection.

2. Group selection narrowly defined. For a trait to be favored by group selection narrowly defined (GSN), it has to be the case that a single mutant cannot invade the population; only when a large proportion of a group is made up of mutants will mutants enjoy a fitness edge relative to the population average. In the example above, the vole-killer mutation spread in the population even when present in only a single individual, so it does not qualify as GSN. Let's change the example a bit. Suppose the farmers are threatened by tigers. If there is a single individual in the population carrying a tiger-killer mutation, that individual will go out tiger hunting and probably end up as tiger food. The mutation will not spread. But suppose that tiger hunting is less dangerous when carried out in the company of others. Then, in a group with a high proportion of individuals carrying the tiger-killer mutation, tiger-killers might actually gain enough by eliminating tigers from the neighborhood to make up for the risks of tiger hunting. If the tiger-killer mutation spread as a result, this would be a case of GSN. Obviously GSN is harder to get started up than GSB.

2a. GSN for altruism. What about non-tiger-killers in groups made up mainly of tiger-killers? They're getting a free ride, while the tiger-killers are acting as altruists. Whether the tiger-killer mutation can persist in the face of these free riders depends on parameters like migration rates and group extinction rates, and on how new groups are formed. I think GSN for altruism is what most sociobiologists have in mind when they criticize Wynne-Edwards-style population regulation arguments and insist that advocates of group selection have to make a case that carriers of group-selected traits lose out in within-group fitness.

2b. GSN for alternative evolutionarily stable states (Boyd & Richerson 1990). Let's change the scenario above slightly. Suppose that non-tiger-hunters in groups with a large proportion of tiger-hunters are not allowed a free ride. They are punished (fined, roughed up, expelled, or excluded from group insurance schemes). And suppose (to make punishment evolutionarily stable) that those who do not contribute to punishing the antisocial are in turn punished. In this case, within-group selection may favor non-tiger-killers in groups with few tiger-killers, and tiger-killers in groups with many tiger-killers. In other words, once a group gets more than some critical proportion of a certain type, it is stable against invasion by the other type; a group can be at either of two alternative evolutionarily stable states (ESSs). But the between-group component of selection is likely to favor groups at the tiger-killer ESS over those stuck at the non-tiger killer ESS, so the former will gradually take over the population. This is not so much group selection for altruism as group selection for participation in a social contract. (Other processes that give rise to alternative ESSs – for example, runaway sexual selection – could also provide the between-group variation that group selection needs.) This form of group selection is not vulnerable to overthrow by small numbers of selfish immigrants the way Type 2a is.

How important are the different types likely to be in evolution? Type 1 is ubiquitous, but it is not clear whether we really want to label it as group selection. Type 2a is likely to be commonest in