

Human groups as adaptive units: toward a permanent consensus

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Foundational changes are taking place in our understanding of human groups. For decades, the biological and social sciences have been dominated by a form of individualism that renders groups as nothing more than collections of self-interested individuals. Now groups themselves are being interpreted as adaptive units, organisms in their own right, in which individuals play supportive roles.

Let me be the first to acknowledge that this new conception of groups is not really new. A long view of scientific and intellectual history reveals that the last few decades have been an exception to the rule. The founding fathers of the human social sciences spoke about groups as organisms as if it were common sense (Wegner 1986). Before them, philosophers and religious believers employed the metaphor of society as organism back to the dawn of recorded history.

Far from robbing recent developments of their novelty, this pedigree only deepens the mystery. How is it possible for one conception of groups to be common sense for so long, for a radically different conception to become common sense, and then for the earlier version to experience a revival? A superficial answer is that ideas are like pendulums that swing back and forth. On the contrary, I believe that the organismic concept of groups will become permanently established, in the same sense that the theory of evolution has become permanently established, even if there will always be a frontier of controversy. In this paper I will attempt to show how the ingredients for a permanent consensus are already at hand.

A theoretical zone of agreement

Despite the radically different conceptions of groups, there are some substantial zones of agreement that provide the basis for a future permanent consensus. The first concerns the theoretical conditions for a group to become an adaptive unit similar to a single organism. Prior to the middle of the 20th century, adaptations were often thought to evolve for the good of the individual, group, species, or ecosystem as if there was no need to distinguish among these units. This position, which now is termed “naive group selectionism”, became the target for criticism by a number of authors, notably G.C. Williams (1966) in his book Adaptation and Natural Selection. A consensus emerged that natural selection at any given level of the biological hierarchy requires a corresponding process of natural selection at that level.

As an example, consider a single group consisting of two types of individual, A and B. Type A individuals behave in a way that increases the fitness of everyone in their group (including themselves) at no cost to themselves. The idea of providing a public good at no private cost might seem unrealistic but is useful for illustrative purposes. Type B individuals are free-riders that enjoy the benefits provided by A-types without providing any benefits of their own. By increasing the fitness of everyone, the frequency of A-types does not change within the group (except by drift). After all, natural selection is based on differences in fitness, which are not present in this example. If providing the public good requires a private cost, then A-types will be less fit than B-types and their frequency within the group will decrease until they ultimately go extinct. More generally, *natural selection within a single group is insensitive to the welfare of the group*. This is one of the fundamental principles that emerged in the middle of the 20th century; it enjoys, and deserves, widespread agreement.

Continuing this example, suppose that there are many groups, not just one, that vary in their frequency of A and B types. Even though the frequency of A does not change within any group (except by drift), groups with a higher frequency of A will

contribute more to the total gene pool than groups with a lower frequency of A. In effect, we have added a process of natural selection at the group level: a population of groups, that vary in their genetic composition, with corresponding variation in their contribution to the gene pool (fitness). Group selection provides the fitness *differences* that were lacking within groups. In the case of a no-cost public good, any variation among groups is sufficient for the A-type to evolve to fixation in the total population, because positive among-group selection is unopposed by within-group selection. If providing a public good requires a private cost, then positive selection at the group level is opposed by negative selection at the individual level and the outcome depends upon the relative strength of the two processes. More generally, *groups can evolve into adaptive units that are designed to maximize their contribution to the total gene pool to the extent that selection among groups prevails against selection within groups*. This is also part of the consensus that emerged in the middle of the 20th century; it remains theoretically valid today (see Sober and Wilson 1998 for a fuller discussion).

A third part of the consensus was that among-group selection is almost invariably weak compared to within-group selection, so that in the vast majority of cases groups cannot be considered adaptive units. Notice that this is an empirical claim, in contrast to the previous two theoretical claims. The first two claims establish the conditions under which group-level adaptations can evolve in principle. The third claim asserts that these conditions seldom exist in the real world.

Everything that I have said so far is part of the received wisdom during the age of individualism that can be found in just about any evolution textbook during the last 40 years. For the purpose of this essay, the important point is that a new consensus can be reached by challenging the empirical claim while retaining the theoretical consensus. The fact that a permanent theoretical consensus has already been established makes the task of establishing a new overall consensus easier.

An empirical zone of agreement

In the previous section I argued that the individualistic conception of human groups can be rejected and the organismic conception accepted on the basis of a theoretical framework that everyone accepts. If an adaptation evolves by group selection, then it is for the good of the group. If I am correct, then the existing disagreement must be empirical in nature. Nevertheless, at a pre-theoretical level there is also widespread empirical agreement about the pervasive cooperative character of human society. Reviews of my recent book Darwin's Cathedral: Evolution, religion and the nature of society (Wilson 2002) vividly illustrate this point. The thesis of this book is that religious groups and other human social organizations are highly cooperative and evolved by genetic and cultural group selection. In one set of commentaries whose authors come from a variety of backgrounds, not everyone agreed about group selection but they did agree with the empirical evidence for religious groups as highly cooperative units. Alvis (2003) stated "I do not doubt his thesis that religious communities can function as adaptive units." Hinde (2003) regarded the empirical claim as "superbly demonstrated". Lease (2003) regarded it as unsurprising and already appreciated within the humanities. Paden (2003) called it "obvious", at least at the level of historical observation. In another book on religion from an evolutionary perspective, Atran (2002) rejects adaptationist hypotheses at both the group and individual level in favor of a byproduct explanation. My hypothesis based on group selection is criticized at length, but when the theoretical dust settles (at least according to Atran) he still acknowledges that "it is embarrassingly obvious that ... religious groups cooperate among themselves to better compete against other groups (p 233)." This quote could easily have come from Alexander (1987), Ridley (1987), or Wright (2000), including the emphasis on between-group competition, but these authors base their views on individual- or gene-level selection rather than group selection or non-adaptive byproduct accounts.

In short, there appears to be nearly universal agreement about the empirical fact of human cooperation within groups and even on the importance of between-group competition as a causative factor. The controversy is about how to explain the accepted empirical fact theoretically. How odd! What I have said in this section seems to conflict flagrantly with what I said in the previous section. How it is possible for everyone to agree theoretically on what counts as a group-level adaptation, for everyone to agree

empirically on the fact of human groups as (largely) cooperative units, and for so much controversy to remain about how to theoretically interpret human cooperation as a group-level adaptation, an individual-level adaptation, a gene-level adaptation, or a nonadaptive byproduct of evolution?

Part of the problem: Logical inconsistency

It might sound suspect and self-serving to say that much of the controversy is based on logically inconsistent arguments that can be dispelled with a little bit of clear thinking. In a vigorous debate among smart people, these problems are quickly dispelled, leaving more interesting and substantial differences of opinion. However, the controversy over the nature of groups is not restricted to a debate among smart informed members of a single group dedicated to the task. It takes place at a much larger spatial, temporal, and disciplinary scale that leaves plenty of room for logical inconsistency. For example, the average college biology student learns little more about group selection than what I provided at the beginning of this essay. Mostly they learn that it is wrong and different from accepted theories such as kin selection and reciprocal altruism. Even their knowledge of the accepted theories is rudimentary. Theoretical literacy is low even among graduate students and faculty in ecology, evolution, and behavior. To re-evaluate group selection, such people would first need to overcome the aura of foolishness and taboo that surrounds the subject. Then they would need to increase their theoretical literacy to the point where they could follow a simple mathematical argument. All of this would take time and effort that they might be unwilling to invest unless they became centrally interested. It would result in endless conversations with peers who have not made the same commitment and the substantial likelihood that manuscripts and grants would be rejected because they invoke group selection. The situation for students and faculty from other disciplines trying to learn about evolution is even worse.

These sociological factors tend to be regarded as boring by those who want to examine the issues on purely scientific grounds. Nevertheless, they are interesting in their own right, especially for philosophers and sociologists of science who wish to achieve a realistic understanding of science as it is actually practiced. I will therefore elaborate on

how there can be a zone of theoretical agreement that nevertheless results in controversy that persists for decades.

The theoretical consensus, as I stated earlier, is that group-level selection is required for groups to evolve into adaptive units. To determine if any particular trait evolves by group selection, the following information is required.

- 1) The groups must be defined.
- 2) The relative fitness of individuals bearing alternative traits within single groups must be examined to evaluate within-group selection.
- 3) The relative fitness of groups in the total population must be examined to evaluate among-group selection.
- 4) The relative strength of within- and among-group selection must be evaluated to determine the role of among-group selection in total evolutionary change.

This follows directly from the theoretical consensus. Anyone who has accepted even the abbreviated account of group selection provided in textbooks should feel compelled to accept these conditions for evaluating group selection. Thus we are still in the zone of theoretical agreement.

Now comes the problem: Many discussions of evolution include the information listed above but do not present it in a way that allows the role of group selection to be evaluated. Instead, group selection is rejected verbally or not mentioned at all and total evolutionary change is attributed to individual-level selection. When the same information is presented as outlined above, group selection proves to be a significant component of total evolutionary change. The rejection of group selection is therefore logically inconsistent. As long as the commonly accepted theoretical framework remains valid, the role of group selection must be acknowledged, based on the empirical information provided.

Elliott Sober and I have extensively discussed this problem (Sober and Wilson 1998), including detailed case studies (e.g., Wilson 1998, 1999, 2000). As a quick way to illustrate the magnitude of the problem, I encourage the reader to listen closely to the next conversation that he or she has about the evolution of any given trait. Very often the

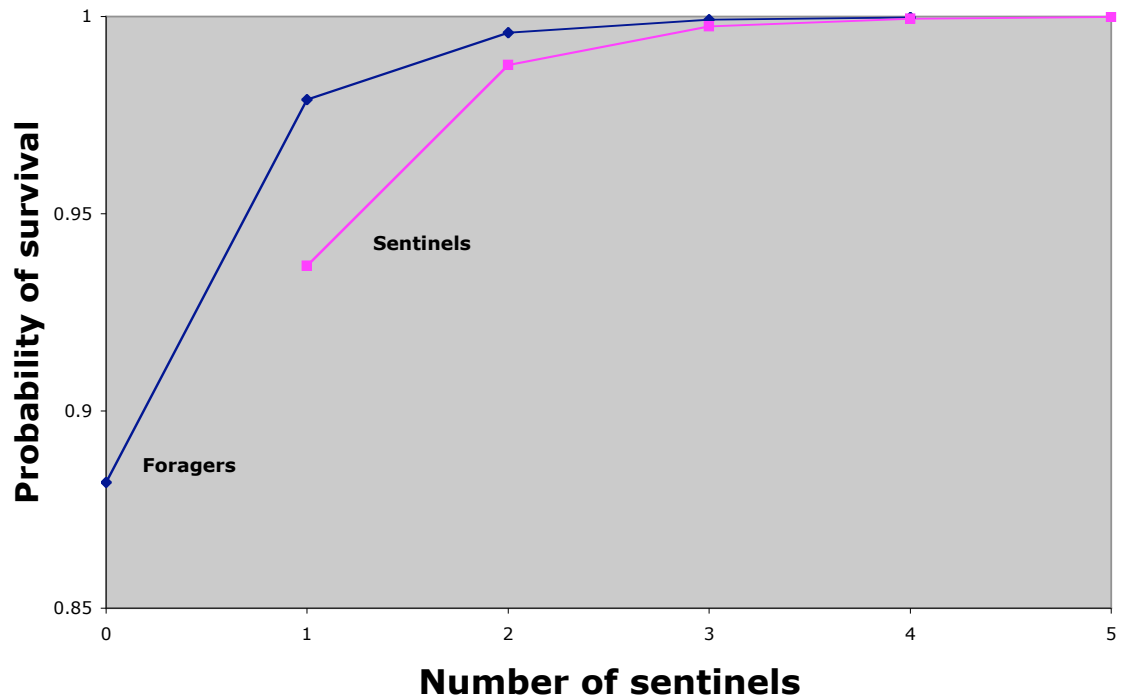
discussion is framed not in terms of evolution per se but in terms of an individual making a decision. Will it receive a higher fitness by adopting trait A or alternative trait B? Whichever trait bestows the highest fitness is assumed to evolve by “individual selection”. This heuristic assumes that “individual selection” will maximize the absolute fitness of the individual, even though everyone knows that natural selection is based on relative fitness and that the evaluation of group selection requires the comparison of relative fitnesses within and among groups.

The assumptions that are required for the absolute fitness criterion (AFC) to correctly predict the outcome of natural selection or to correspond to within-group selection are usually unstated and unquestioned. Returning to our example of the no-cost public good, an individual would increase its absolute fitness by adopting trait A compared to trait B, but not its relative fitness within its own group. Multiple groups and variation among groups are required for A to evolve. Given these conditions, the AFC does correctly predict the outcome of natural selection (the A-trait does evolve), but mistakenly attributes the outcome to within-group selection. In other cases the AFC simply comes to the wrong conclusion about what evolves (Wilson 2004).

This problem exists not only at the level of casual conversation but at the highest levels of scientific discourse. A recent model of sentinel behavior provides a sterling example (Bednekoff 1997). In numerous species of birds and mammals, a single individual scans for predators, often from an exposed location, while other members of its group forage for food. Along with alarm calls, sentinel behavior is a classic example of altruism that seems to require group selection, with a shared benefit (enhanced protection from predators) and two potential private costs; exposure to predators and inability to feed. Bednekoff’s model attracted attention because it interpreted sentinel behavior as “safe” and “selfish” for the sentinel rather than altruistic.

The core of Bednekoff’s model is shown in the accompanying figure, which portrays the fitness of sentinels and foragers (y-axis) in a single group of five individuals in which some number between one and five act as sentinels (x-axis). Each forager fails to detect a predator attack with probability V and each sentinel fails to detect a predator attack with the smaller probability V/a ($a > 1$). The term a therefore represents the enhanced protection afforded by the sentinel. Detection by either foragers or sentinels is

assumed to be noticed by the whole group, so the collective probability of failing to detect an attack is $V^F(V/a)^S$, where F is the number of foragers and S is the number of sentinels in the group. The predator is assumed to be successful if it remains undetected and the individual that is actually killed is determined by a lottery in which each forager holds 1 “ticket” and each sentinel holds b “tickets” ($b > 1$). The term b therefore measures the relative risk of a sentinel if the predator remains undetected. Because a appears in both fitness equations and b appears only in the numerator of the sentinel’s fitness, sentinels provide a public good at their own private cost. This is shown graphically by the two curves in which the fitness of both foragers and sentinels increases with the number of sentinels in the group (positive slopes) but the fitness of sentinels is always less than the fitness of foragers (one curve entirely below the other). Equations and graphs similar to these are typically used to study altruism. The graph charts values for $F+S=5$, $V=.9$, $a=4$ and $b=3$.



$$\text{Forager's probability of survival} = 1 - [V^F(V/a)^S][1/(F+bS)]$$

$$\text{Sentinel's probability of survival} = 1 - [V^F(V/a)^S][b/(F+bS)]$$

I have presented this model in detail to show that it includes all of the information required to identify sentinel behavior as a group-level adaptation, at least within the context of the model. First, the groups are clearly defined as the set of individuals who influence each other's fitness with respect to the evolving trait. Second, it is clear that sentinels are less fit than foragers within any single group. Third, it is clear that groups with more sentinels contribute more to the total gene pool than groups with fewer sentinels. Fourth, the relative strength of within- and among-group selection will depend on the amount of variation among groups and on other details of population structure, but it is clear that whenever the sentinel behavior does evolve, it will be on the strength of among-group selection, since it is selectively disadvantageous within groups. Given all of this, how can Bednekoff (197) interpret the sentinel behavior as "safe" and "selfish"?

The answer is that an individual can increase its absolute fitness by becoming a sentinel, even as it decreases its relative fitness within its group. For example, imagine a

forager in a group without sentinels deciding how to behave. As a forager, its probability of survival is approximately 0.88 (see figure 1). If it becomes a sentinel in a group with one sentinel (itself), its probability of survival will be approximately 0.94. It is on this basis that Bednekoff called sentinel behavior safe and selfish. Subsequent empirical studies claiming to support the model were widely reported in prestigious journals such as Science (Clutton-Brock et al. 1999) and the popular press. The newsworthiness of this research is that something previously regarded as altruistic turns out to be selfish after all, yet the entire result is based on a definitional shift from relative to absolute fitness. The information that establishes the trait as a group-level adaptation is there for everyone to see, but few people bother because they unthinkingly equate “individual selection” with the maximization of absolute fitness.

This is the tip of an iceberg of evolutionary thinking, both formal and informal, that invokes group selection without knowing it. There is no logical justification for this kind of “controversy”. Sociologically, evolutionary biologists can presently be divided into roughly three categories. The first has become fully comfortable with multilevel selection and wonders what all the fuss is about. After all, don’t the models and the empirical data clearly indicate the importance of among-group selection? The second category acts as if nothing has changed since the 1960’s, which can be seen by the formulaic statements about the rejection of group selection and failure to discuss the recent literature. The third category has lapsed into silence about group selection, as if it never existed in the history of evolutionary thought. These authors are presumably aware that something has happened that challenges the earlier rejection of group selection, but evidently they don’t want to get involved. Who cares, as long as their models correctly predict the outcome of evolution? Thus, Bednekoff (1997) does not mention the term group selection, even though the ghost of group selection is present in the author’s rejection of the old interpretation of sentinel behavior as altruistic. As another example, Giraldeau and Caraco (2000) wrote an entire book on group foraging without mentioning group selection, much less evaluating their models or empirical data in a way that would enable the role of group selection to be identified.

A fourth category does not exist. No person today, to my knowledge, has accepted the theoretical framework that I have described as the zone of agreement, gathered the

information required to evaluate the role of group selection, and concluded that virtually all traits evolve by within-group selection. That was the claim that became the foundation for the “theory of individual selection” in the middle of the 20th century, and it currently stands empty for the best of reasons. It cannot be sustained by plausible theoretical models and the empirical evidence. That is why I am confident that an overall permanent consensus can be established on scientific grounds, whatever the sociological challenges.

I will end this section with a brief discussion of the recent philosophical literature on multilevel selection, represented by forums published in the *Journal of Consciousness Studies* (Volume 7(1), 2000) and the journal *Biology and Philosophy* (Volume 17(4), 2002). These authors come close to being a single group of smart informed people dedicated to the task. If they can’t reach a consensus, what hope for the wider community? My reading of the literature indicates that a consensus has been reached on the most fundamental issues and that the “frontier of controversy” has moved on to issues that participants of the debate in the 1960’s would have difficulty recognizing. For example, there seems to be complete agreement that multilevel selection theory is logically consistent and indicates an important role for group selection in the evolution of many traits. The question now centers on whether alternative ways of working with the same information, for example by averaging the fitness of individuals across groups or the fitness of genes across individuals and groups, can be considered a form of individualism alongside multilevel selection. Whatever the answer to this question, it is not the same question that was being asked earlier. There will always be a frontier of controversy, but it is important to acknowledge the kind of progress that renders past frontiers uncontroversial. That kind of progress has occurred among philosophers of biology and theoretical biologists who remain interested in the subject of group selection, as opposed to ignoring its existence as a fundamental issue in evolutionary biology.

Psychological mechanisms and indirect products of natural selection

After the logical inconsistencies discussed in the previous section are acknowledged and avoided, another set of issues remains. Suppose we observe a behavior that clearly provides a public good at private cost. Our nested series of relative fitness comparisons

reveals that the public good providers are less fit than non-providers within their own groups but that groups with providers are more fit than groups without providers. The behavior counts as a group-level adaptation in terms of present-day fitness effects, but we still need to know how the behavior arose historically. After all, most evolutionary definitions of adaptation require not only an appropriate fit to the environment, but also the historical process of natural selection that brings the trait about. Consider the following possibilities (which are not intended to be mutually exclusive).

P1) The behavior that provides the public good evolved as the direct product of genetic group selection. Behavioral differences reflect genetic differences, the behavior is selectively disadvantageous within groups, and evolves by virtue of the differential fitness of groups.

P2) The behavior evolves as a direct product of cultural group selection. Behavioral differences do not reflect genetic differences but the behavior is still transmitted from one individual to another by cultural inheritance mechanisms. As in the previous case, the behavior is selectively disadvantageous within groups and evolves only by virtue of the differential fitness of groups.

P3) The behavior originates and spreads by psychological processes rather than an evolutionary process. For example, suppose that people in one group got together to decide and implement the best policy, which was then quickly imitated by the members of other groups. The behavior is adaptive at the group level in terms of fitness effects but did not evolve by a group selection process, genetic or cultural.

P4) The psychological process could be conscious or unconscious. Conscious decision-making processes are the tip of an iceberg of unconscious processes that are often very sophisticated, despite our unawareness of them (Barkow et al 1992, T.D. Wilson 2002).

P5) The psychological process could count as altruistic or selfish as psychologists and philosophers have traditionally used these terms (Sober and Wilson 1998). For example,

according to the standard portrayal, psychological egoists strive to maximize their welfare without regard to others, not in comparison to members of their own group, and would decide to provide a public good if their share exceeds their private cost. This behavior would be behaviorally disadvantageous within groups, requiring a process of group selection to evolve, but it would be motivated by a psychological process that counts as egoistic.

The behavior is straightforwardly a group-level adaptation according to P1 and P2 because it arises directly from an historical process of group selection. The distinction between genetic and cultural inheritance has no bearing on the status of the behavior as a group-level adaptation. A direct process of natural selection is lacking in P3-P5. To proceed further we need to think about the evolution of the psychological processes that directly account for the behavior. Consider the following analogy. Many organisms have evolved to be cryptic to avoid detection by their predators and/or prey. In some cases the individuals have no control over their appearance; they are simply born a certain way. In other cases the individuals do have control, such as a chameleon's wonderful ability to match its background within minutes. Is the green color of a chameleon against a green background an adaptation? No, in the sense that it arose from a flexible physiological process rather than a process of natural selection. Yes, in the sense that the flexible physiological process evolved by natural selection.

Returning to human psychology, it is easy to imagine a mind designed entirely by within-group selection. Such a mind would routinely produce behaviors that maximize relative fitness within groups and would seldom produce behaviors that benefit the group at private expense, except as an occasional mistake. If people routinely produce behaviors that qualify as group-level adaptations in terms of fitness effects, then the underlying psychological mechanisms are likely to be a (partial) product of group-level selection. To summarize, if a behavior that qualifies as a group-level adaptation on the basis of fitness effects exists by virtue of psychological processes such as decision making and imitation, rather than by an evolutionary process, that does not by itself constitute an argument against group-level adaptation. Instead, it shifts attention to the evolution of the

psychological processes. If the behavior is a typical product of the psychological processes, then the processes are likely a product of group-level selection.

These comments apply to all of the psychological possibilities (P3-P5) outlined above. What about the distinction between conscious vs. unconscious (P4) and altruistic vs. selfish (P5) psychological processes? Neither of these distinctions influences the status of the behavior or the psychological processes as a group-level adaptation. It is commonplace in evolutionary biology to expect a given phenotypic trait to potentially evolve by more than one proximate mechanism. If the trait evolves by among-group selection, it is a group-level adaptation regardless of the particular proximate mechanism that evolves. P3-P5 represent alternative proximate mechanisms.

Advancing the frontier of controversy

I began this essay by saying that the ingredients for a permanent consensus on human groups as adaptive units are already at hand. There is a theoretical zone of agreement on what constitutes a group-level adaptation and an empirical zone of agreement about widespread cooperation in human groups. Despite decades of resistance, it is possible to connect these two zones, concluding that group-level selection has been a very important evolutionary force in human evolution, accounting for our groupish nature. Of course, within-group selection has also been an important force, accounting for our tendency to subvert groups and our difficulty functioning cooperatively in groups beyond a certain scale. Multilevel selection theory is ideally suited to explain human nature in all its prosocial and antisocial complexity.

The importance of reaching a consensus on something so basic is that it allows us to advance the frontier of controversy to more refined issues. In this spirit, I conclude by describing a number of issues that I regard as far more interesting and worthy of attention than the raw fact of group-level selection.

- 1) *The importance of ongoing cultural group selection.* Part of the functionality of modern human groups has arisen by cultural group selection and was never planned by anybody. We behave in ways that are smart but we don't have a

glimmer of awareness about what, how or why, prior to scientific investigation. Furthermore, well-documented examples of cultural group selection exist in the social science literature, although they have seldom been associated with the evolutionary issues discussed in this essay (see Wilson 2002 for examples).

- 2) *The importance of genetic group selection.* Robert Boyd, who has championed cultural group selection for as long as I have championed group selection in general, has stated that the received wisdom about genetic group selection is correct and that culture is required to make group selection a significant evolutionary force (most recently summarized in Richerson and Boyd 2004). One basis for Boyd's claim is his model of cultural group selection with Peter Richerson (Boyd and Richerson 1985), in which a conformity trait evolves by within-group selection as an adaptation to varying environments, with consequences for cultural group selection that are initially a byproduct. Another basis for Boyd's claim is semantic. He acknowledges that so-called alternatives to group selection, such as kin selection theory and evolutionary game theory, are themselves multilevel selection models that include within- and among-group selection. However, he thinks cultural group selection is the only important new context in which group selection occurs, other than the contexts that are already familiar in terms of kin selection and reciprocity. For example, he would claim that group selection is never important in large groups of unrelated individuals in the absence of culture. I disagree for reasons that are presented in detail elsewhere (Sober and Wilson 1998, Wilson 2004). Culture is one kind of complex process that can radically alter the partitioning of phenotypic variation within and among groups. Other non-cultural processes exist that have the same effect, for example in microbial ecosystems (Swenson and Wilson 2000a,b) or in interactions among insects (Rissing and Pollock 1989). With respect to human evolution, the traits that make cultural group selection possible have a genetic basis that almost certainly evolved at least in part by genetic group selection, Boyd and Richerson's (1985) particular model notwithstanding (e.g., Wilson and Kniffin 1999). Gene-culture co-evolution is the hallmark of the theory developed by Boyd and

Richerson, but a consensus has yet to form on whether one or both are multilevel processes. This current “frontier of controversy” is more interesting and substantive than arguing over the raw fact of group selection.

- 3) *A new look at conscious psychological processes.* Conscious intentional thought is undeniably important in the social organization of human groups. To give an example that I discuss in detail elsewhere (Wilson 2002, ch 3), John Calvin and his contemporaries during the Protestant Reformation were in part savvy social planners thinking in pragmatic terms. As another example, Boehm (1996) searched the anthropological literature for examples in which indigenous people were forced to make an emergency decision and an anthropologist was there to observe what happened. In each case there is a pragmatic discussion of costs and benefits that we would recognize as rational, with minimal reference to superstition, supernatural agents, and so on. However, conscious intentional thought is not the same as self-interested thought. In all of the above-cited cases, the question was what the group should do as a collective unit. Exploitation and conflicts of interest within the group were often part of the discussion and resolved in a way that minimized the potential for within-group selection. For example, either the group would reach a consensus about what to do that eliminated behavioral variation within groups (e.g., everyone goes to war), or it would regulate the fitness consequences, such as by agreeing to punish freeloaders or to restrict the benefits of public goods to those who generated them (e.g., only those who go to war can enjoy the spoils of war). In short, when the elements of intentional thought are examined in terms of the nested series of fitness comparisons described by multilevel selection theory, they emerge largely as group-level adaptations that succeed by increasing the fitness of groups as corporate units, not the fitness of some individuals compared to others within the same group.
- 4) *The importance of unconscious psychological processes.* The importance of intentional thought notwithstanding, there are almost certainly many

psychological processes relevant to group-level adaptation that are beneath conscious awareness, simply because this is true for human mentality in general (Barkow et al 1992, T.D. Wilson 2002). Unlike adaptations that evolved directly by cultural group selection, somebody thought them up. Nevertheless, we don't have a glimmer of awareness about them prior to scientific investigation.

- 5) *The possibility of group-level cognition.* Human cognition is usually assumed to be an individual-level process, even if the outcome of the cognition is adaptive at the group level (e.g., an individual deciding to provide a public good at private expense). Another possibility is that the group becomes the cognitive unit, with social interactions comparable to neuronal interactions. The concept of a “group mind” might sound like science fiction but its likelihood follows directly from multilevel selection theory, has been well documented in social insects, and is fully plausible for human groups (Wilson 1997, Wilson, Timmel and Miller 2004).

- 6) *The importance and plurality of non-egoistic psychological motives.* The idea that all human motives are psychologically egoistic is almost certainly false. Motives are proximate mechanisms that evolve by virtue of the behaviors they cause. It is possible for egoistic motives to produce group- and other-oriented behaviors in principle, but not as efficiently as non-egoistic motives (Sober and Wilson 1998). The very idea of a single overarching motive is outdated. If the kind of modularity emphasized by evolutionary psychologists (Barkow et al. 1992) is even partially correct, there can be different evolved motives for different situations and there is no theoretical reason why all of them should be egoistic. In addition to a plurality of motives within individuals, evolutionary models predict that human populations should consist of a mix of behavioral strategies, such as cheaters, cooperators who punish, and cooperators who don't punish (Fehr and Fischbacher 2003). If motives are strategies that compete against each other in game theoretic fashion, then the outcome will almost certainly be a community of coexisting motives that succeed in different ways, not a single overarching motive.

7) *A subordinate role for proximate mechanisms in moral philosophy.* Multilevel selection theory is ideal for studying morality because it does not insist that morality (along with everything else) is a variety of self-interest. Philosophical discussions of morality often concentrate almost exclusively on how people think about their conduct rather than on how they behave. This emphasis ignores the relationship between proximate and ultimate causation in evolutionary biology. As mentioned previously, it is common for a single phenotypic trait to evolve via more than one proximate mechanism. To pick an imaginary human example, a behavior considered moral could evolve via a psychologically egoistic mechanism, a psychologically altruistic mechanism, a mechanism that is internalized so that is voluntarily performed, a mechanism that is externalized as a form of social control, and so on. Every evolved behavior requires a proximate mechanism, but the particular proximate mechanism that evolves is usually considered a minor issue and often a matter of chance. Why then, is a particular proximate mechanism being treated as the basis of morality, when others can potentially motivate the same human conduct? This is only one example of how evolutionary theory in general and multilevel selection in particular will require fundamental changes in moral philosophy.

How to Begin

These and other issues are already being discussed by those comfortable with multilevel selection theory and can occupy center stage for everyone after the tedious debate over the raw fact of group selection is over. There is nothing intrinsically difficult about multilevel selection theory. Dennett (2002) called it “mind-bogglingly complex”, but that is only against the background of what preceded it. The history of science is full of ideas that initially appeared mind-boggling, only to become the new common sense. In my experience, the average college student who approaches the subject with a fresh mind can develop a workable set of intuitions in a single semester. These include thinking about groups as potentially adaptive units, in the same way that everyone is currently

accustomed to thinking about individuals, making the appropriate relative fitness comparisons, and thinking clearly about proximate and ultimate causation. Advanced competence in multilevel selection theory is no more difficult than for other theoretical frameworks, such as population genetics, inclusive fitness theory, and evolutionary game theory. I look forward to the day when the basic intuitions of everyone who thinks about evolution and the advanced competence of practicing scientists become the new and permanent consensus.

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