The Role Of Group Selection In Human Psychological Evolution

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It is impossible to evaluate the role of group selection in human psychological evolution without taking the turbulent history of the subject into account. The theory of group selection begins with Darwin, who realized that altruistic behaviors are selectively disadvantageous within groups and require a process of selection among groups to evolve. In the following famous passage from *Descent of Man*, he used group selection to explain the evolution of behaviors associated with human morality: "It must not be forgotten that although a high standard of morality gives but a slight or no advantage to each individual man and his children over other men of the same tribe, yet that an increase in the number of well-endowed men and advancement in the standard of morality will certainly give an immense advantage to one tribe over another (Darwin 1871, p. 166) ."

Darwin's insight was shared by the first architects of population genetics theory, including Ronald Fisher, Sewall Wright, and J.B. S. Haldane (Sober and Wilson 1998). Unfortunately, many other biologists naively assumed that adaptations can evolve "for the good of the group" without requiring special conditions. This position was widely criticized in the 1960's, especially by G.C. Williams (1966) in his book *Adaptation and Natural Selection*. Williams accepted multilevel selection as a theoretical framework, agreeing with Darwin, Fisher, Wright, and Haldane that group-level adaptations can evolve only by a process of group-level selection and are often opposed by selection among individuals within groups. Williams then made an additional claim that group selection can be ignored because it is almost invariably weak, compared to within-group

selection. This additional claim turned multilevel selection into what became known as "the theory of individual selection."

Williams and other critics were so successful that group selection became a heretical concept, as anyone who lived through the period can attest. All of the theories that became the foundation for study of social behavior, including inclusive fitness theory, reciprocal altruism, game theory, and selfish gene theory, were developed as alternatives to group selection. It became almost mandatory for the authors of books and articles to assure their readers that group selection was not being invoked.

The rejection of group selection was especially problematic for the study of human evolution. Anyone who studies humans must acknowledge that we are a highly cooperative species and that our cooperation extends beyond genetic relatives and narrow reciprocators. It is also inescapably true that human evolution has been influenced by interactions among groups in addition to interactions within groups. How can these facts be reconciled with the claim that groups are not important units of selection?

The current literature is in complete disarray on this issue. Some authors still warn their readers about group selection, as if nothing has changed since the 60's. Other authors regard group selection as an important force in human evolution, especially when it comes to cultural evolution. Still others avoid mentioning the term group selection, as if it never existed in the history of evolutionary biology. There is a resolution to this controversy, but it requires a "back to basics" approach that the field has a whole has been reluctant to undertake. The rest of this essay will show how Darwin's original insight was correct and how more recent advances in knowledge can be better understood within the context of multilevel selection theory than as an alternative.

How to determine levels of selection

Multilevel selection theory is a stepwise procedure for calculating evolutionary change in a population that is subdivided into groups. The first step is to identify the groups of locally interacting individuals and other aspects of the population structure, such as how the groups are formed, dispersal among groups, and so on. The second step is to determine the direction and intensity of natural selection within single groups. In Darwin's passage about human morality, he conjectured that moral traits do not increase

in frequency within single groups and might well decrease in frequency, compared to the traits associated with immorality. The third step is to determine the direction and intensity of natural selection among groups in the total population. If some groups persist longer and produce more dispersers than other groups, then this will alter the frequency of alternative traits in the total population, as surely as evolutionary change within single groups. Darwin conjectured that groups of moral individuals contribute more to the total population than groups of immoral individuals. The final outcome of evolution depends upon the relative strength of within and between group selection, like a final vector made up of two component vectors. Darwin conjectured that group selection was sufficiently strong to favor the traits associated with human morality, despite their selective neutrality or disadvantage within single groups. Subsequent theories of multilevel selection might seem complicated because they are stated in mathematical form, but they all preserve the very simple logic of Darwin's passage, which is easy for anyone to understand.

Why group selection was rejected in the 1960's

The rejection of group selection was based upon three arguments, like the legs of a stool. First, theoretical models available at the time made between-group selection appear weak compared to within-group selection. Second, there was no compelling empirical evidence in favor of group selection. Third, other theoretical frameworks such as inclusive fitness theory, game theory, and selfish gene theory seemed to offer more robust explanations of cooperation and altruism without invoking group selection. These arguments appeared invincible at the time, but all three began to be questioned, even as early as the 1970's. When we examine their status in the 21st century, it becomes obvious that *the original consensus was in error*, however difficult it might be to acknowledge the fact in sociological terms.

The theoretical plausibility of group selection

I often encounter the skeptical attitude that theoretical models count for little in the absence of good hard evidence, but a careful reading of the literature reveals that the 1960's consensus was based almost entirely on theoretical plausibility arguments. The selective advantage of selfishness within groups just seemed more robust than the group-

level advantages of altruism. It therefore means something when group selection became more plausible on the basis of subsequent theoretical models. For example, all of the early models assumed that altruistic and selfish behaviors are coded directly by altruistic and selfish genes, which causes phenotypic variation within and among groups to become tightly coupled with genetic variation. Evolutionary psychologists might verbally reject simplistic assumptions about genetic determinism, but those very assumptions are built into the theoretical models. As soon as we make the genotype-phenotype relationship more complicated, via mechanisms such as individual phenotypic plasticity, social norms reinforced by punishment, and social transmission processes, between-group selection becomes a force to be reckoned with, even in large groups of unrelated individuals (Wilson 2004, Richerson and Boyd 2004). In general, group selection can no longer be rejected on the basis of its theoretical implausibility, especially in the case of human evolution.

The empirical evidence for group selection

The empirical evidence in favor of group selection might have been slim in the 1960's, but the evidence against group selection was also slim. Williams (1966) used the theoretical implausibility of group selection to argue that any hypothesis framed in terms of individual selection—no matter how speculative—is more parsimonious and should therefore be preferred to an hypothesis based on group selection. Arguments based on parsimony are weak at best and become completely invalid when alternative hypotheses are equally plausible. Would any ecologist argue on the basis of parsimony that competition is more important than predation? Both are plausible and their relative importance must be determined empirically on a case-by-case basis. In just the same way, the direction and strength of within- and between-group selection must be determined on a case-by-case basis if both are theoretically plausible.

The closest that Williams (1966) came to a rigorous empirical test was for sex ratios, leading him to predict that female biased sex ratios would provide evidence for group selection. The subsequent discovery of many examples of female-biased sex ratios led Williams to accept the evidence for group selection, stating in 1992 that "I think it desirable…to realize that selection in female-biased Mendelian populations favors males,

and that it is only the selection among such groups that can favor the female bias." Williams also acknowledged the importance of group selection in disease evolution as part of his more general interest in Darwinian medicine, stating in 1991 that "the evolutionary outcome will depend on the relative strengths of within-host and between-host competition in pathogen evolution." See Sober and Wilson (1998, ch 1-3) for other empirical examples of group selection and more detailed discussions of these examples.

Some of the best recent evidence for group selection comes from microbial organisms, in part because they are such elegant systems for ecological and evolutionary research spanning many generations. There is no doubt whatsoever that the problems of altruism and selfishness that Darwin addressed in his passage on human morality, and which have traditionally been studied in insects and social vertebrates, also exist in microbial organisms. Moreover, microbial evolution is undeniably influenced by between-group selection in addition to within-group selection (e.g,. Velicer 2003). The claim that group selection is invariably weak is just plain false on the basis of empirical evidence, requiring an evaluation on a case-by-case basis.

Are the alternative theories really alternatives?

No matter what they are called, all evolutionary models of social behavior share a certain number of core assumptions. All assume that social interactions take place within multiple groups, because this is a biological reality that cannot be ignored. All converge on the same definition of groups for any particular trait (such as sentinel behavior or resource utilization), or else the calculation of fitness will simply be incorrect. If social interactions take place in groups of N=10, 2-person game theory won't do. Once the existence of multiple groups is acknowledged and details of the population structure are determined on the basis of the biology of the situation, the basic logic of multilevel selection theory can be applied, no matter what the model is called. In virtually all cases, the traits regarded as altruistic or cooperative are selectively disadvantageous within groups and require between-group selection to evolve, exactly as Darwin conjectured in his passage about human morality. The main exception to this rule concerns models that result in multiple local equilibria, all of which are internally stable by definition. In this

case, group selection is required to favor local equilibria that function best at the group level, which is sometimes called "equilibrium selection."

The fact that all evolutionary models of social behavior are multi-group models that obey the simple logic of multilevel selection does not detract from their significance. The insights that we attribute to inclusive fitness theory, game theory, and other theoretical frameworks remain as important as ever, but can be understood in terms of the parameters of multilevel selection theory (such as the balance between levels of selection), without requiring additional parameters. In addition, a single unified conceptual framework reveals new possibilities, such as complex interactions leading to substantial phenotypic variation among large randomly formed groups (Wilson 2004).

Major Transitions In Evolution

A major event in evolutionary theory occurred with the discovery that individual organisms are the social groups of past ages. Evolution proceeds not only by small mutational change, but also by groups and symbiotic communities becoming so integrated that they become higher-level organisms in their own right. Despite multilevel selection theory's turbulent history, it is the accepted theoretical framework for studying major transitions. There is universal agreement that selection occurs within and among groups, that the balance between levels of selection can itself evolve, and that a major transition occurs when selection within groups is suppressed, enabling selection among groups to dominate the final vector of evolutionary change. Genetic and developmental phenomena such as chromosomes, the rules of meiosis, a single cell stage of the life cycle, the early sequestration of the germ line, and programmed death of cell lineages are interpreted as mechanisms for stabilizing the organism and preventing it from becoming a mere group of evolving elements. The evolution of social insect colonies also falls within the paradigm, with genetic relatedness only one of several factors that can be understood in terms of multilevel selection without requiring additional parameters. As Wilson and Holldobler (2005) put it in a recent review:"Group selection is the strong binding force in eusocial evolution."

Human Evolution As a Major Transition

The paradigm of major transitions did not emerge until the 1970's and didn't become generalized until the 1990's, with books such as *The Major Transitions of Evolution* (Maynard Smith and Szathmary 1995). Even though these developments are very recent, it is becoming clear that human evolution falls within the paradigm. Human moral systems can be regarded as mechanisms that suppress selection within groups, enabling between-group selection to become the primarily evolutionary force, just like chromosomes and the rules of meiosis (Boehm 1999). Our capacities for social transmission, language, and other forms of symbolic thought are fundamentally communal activities that required a shift in the balance between levels of selection before they could evolve. The human major transition was a rare event, but once established it enabled our species to achieve worldwide ecological dominance. Wilson and Holldobler (2005, p. 13371) stress the parallels with social insect evolution as follows: "Rarity of occurrence and unusual pre-adaptations characterized the early species of *Homo* and were followed in a similar manner during the advancements of the ants and termites by the spectacular ecological success and preemptive exclusion of competing forms by *Homo sapiens*. "

One reason that group selection is an important force in human evolution is because cultural processes have a way of increasing phenotypic variation among groups and decreasing it within groups. If a new behavior arises by a genetic mutation, it remains at a low frequency within its group in the absence of clustering mechanisms such as associations among kin. If a new behavior arises by a cultural mutation, it can quickly becoming the most common behavior within the group. Evolutionary biologists who study cultural evolution are nearly unanimous about the importance of cultural group selection in human evolution (e.g, Richerson and Boyd 2004).

On the need for a new consensus

Making a decision typically involves encouraging diversity at the beginning to evaluate alternatives, but then discouraging diversity toward the end to achieve closure and to act upon the final decision. It can be very difficult to revisit an important decision that has been made and acted upon, but that is precisely what needs to be done in the case

of the 1960's consensus about group selection (Wilson 2006). It might seem amazing that multilevel selection can be revived and even become the unifying theoretical framework for sociobiology, until we realize that Williams and others always accepted its basic logic. The passages quoted above show how easily Williams himself reverted back to multilevel selection thinking, once he decided that group selection is a significant evolutionary force for specific traits such as sex ratio and disease virulence. Evolutionary psychologists need to make the same decision for the traits that they study. Darwin was essentially right, and multilevel selection provides a way to understand our groupish nature at face value.

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