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RETHINKING THE THEORETICAL FOUNDATION
OF SOCIOBIOLOGY

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ABSTRACT

Current sociobiology is in theoretical disarray, with a diversity of frameworks that are poorly related to each other. Part of the problem is a reluctance to revisit the pivotal events that took place during the 1960s, including the rejection of group selection and the development of alternative theoretical frameworks to explain the evolution of cooperative and altruistic behaviors. In this article, we take a "back to basics" approach, explaining what group selection is, why its rejection was regarded as so important, and how it has been revived based on a more careful formulation and subsequent research. Multilevel selection theory (including group selection) provides an elegant theoretical foundation for sociobiology in the future, once its turbulent past is appropriately understood.

D ARWIN perceived a fundamental problem of social life and its potential solution in the following famous passage from *Descent of Man* (1871:166):

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 the other men

of the same tribe . . . an increase in the number of well-endowed men and an advancement in the standard of morality will certainly give an immense advantage to one tribe over another.

The problem is that for a social group to function as an adaptive unit, its members must do things for each other. Yet, these group-advantageous behaviors seldom maximize relative fitness within the social group. The solution, according to Darwin, is that natural selection takes place at more than one level of the biological hierarchy. Selfish individuals might out-compete altruists within groups, but internally altruistic groups out-compete selfish groups. This is the essential logic of what has become known as multilevel selection theory.

Darwin's insight would seem to provide an elegant theoretical foundation for sociobiology, but that is not what happened, as anyone familiar with the subject knows. Instead, group selection was widely rejected in the 1960s and other theoretical frameworks were developed to explain the evolution of altruism and cooperation in more individualistic terms. The following passage from George C Williams's book, *Adaptation and Natural Selection* (1966:92–93), illustrates the tenor of the times, which seemed to make the rejection of group selection a pivotal event in the history of evolutionary thought:

> It is universally conceded by those who have seriously concerned themselves with this problem . . . that such group-related adaptations must be attributed to the natural selection of alternative *groups* of individuals and that the natural selection of alternative alleles within populations will be opposed to this development. I am in entire agreement with the reasoning behind this conclusion. Only by a theory of between-group selection could we achieve a scientific explanation of group-related adaptations. However, I would question one of the premises on which the reasoning is based. Chapters 5 to 8 will be primarily a defense of the thesis that group-related adaptations do not, in fact, exist. A *group* in this discussion should be understood to mean something other than a family and to be composed of individuals that need not be closely related.

Forty years later, this clarity has been lost. In the current sociobiological literature, it is easy to find the following contradictory positions, side by side in the same journals and bookshelves:

- Nothing has changed since the 1960s.
- Multilevel selection theory (including group selection) has been fully revived.
- There is a "new" multilevel selection theory that bears little relationship to the "old" theory.
- Group selection is not mentioned, as if it never existed in the history of evolutionary thought.

Part of this confusion can be explained in terms of the diffusion of knowledge. It takes time for the newest developments in theoretical biology to reach scientists who conduct empirical research, and longer still to reach diverse audiences who receive their information third, fourth, and fifth hand. However, part of the confusion continues to exist at the highest level of scientific discourse, as we will show.

We think that sociobiology's theoretical foundation can be as clear today as it appeared to be in the 1960s, but only if we go back to the beginning and review the basic logic of multilevel selection, what appeared to be at stake in the 1960s, and why the original rejection of group selection must be re-evaluated on the basis of subsequent research. Everyone can benefit from this "back to basics" approach, from the most advanced theorists to students learning about sociobiology for the first time.

A Word About Tainted Words

It is a natural human tendency to avoid associating oneself with people or ideas that have acquired a bad reputation in the past. Thus, there are evolutionists who study social behavior, but avoid the term "sociobiology," or who study psychology, but avoid the term "evolutionary psychology," because of particular ideas that were associated with these terms in the past, including their supposed

political implications. At a broader scale, there are people who avoid the word "evolution" because of past negative associations, even though they are clearly talking about evolutionary processes. We think that this very understandable temptation needs to be resisted in the case of scientific terminology, because the short-term gain for the user (avoiding negative associations) results in long-term confusion for the field as a whole (a proliferation of terms that mean the same thing). The problem has been especially severe for multilevel selection theory because many evolutionists have felt that their very careers would be jeopardized if they invoked group selection. In some cases, their fears were well founded; we could provide numerous examples of colleagues whose articles and grant proposals were rejected when stated in terms of multilevel selection theory, and then accepted when restated using other terms. In this article, we define our terms at face value, regardless of past associations: sociobiology is the study of social behavior from a biological perspective, group selection is the evolution of traits based on the differential survival and reproduction of groups, and so on. Returning to face-value definitions is a first step toward resolving the confusion that plagues the modern sociobiological literature (see also Foster et al. 2007).

From an evolutionary perspective, a behavior can be regarded as social whenever it influences the fitness of other individuals in addition to the actor. Social behaviors need not be *pro*social; aggression fits the definition as does cooperation. Also, the interactions need not be direct; a feeding behavior that reduces the fitness of others by depleting their resources counts as social. Even genetic and developmental interactions within a single individual can be regarded as social, since the organisms of today are now known to be the social groups of past ages, as we will describe in more detail below. Narrower definitions of social behavior might be useful for some purposes, but the important point to keep in mind is that the concepts reviewed in this article apply to any trait that influences the fitness of others in addition to the actor, regardless of how "social" these traits might appear in the intuitive sense.

THE HISTORY AND BASIC LOGIC OF MULTILEVEL SELECTION THEORY

During evolution by natural selection, a heritable trait that increases the fitness of others in a group (or the group at a whole) at the expense of the individual possessing the trait will decline in frequency within the group. This is the fundamental problem that Darwin identified for traits associated with human morality, and it applies with equal force to group-advantageous traits in other species. It is simply a fact of social life that individuals must do things for each other to function successfully as a group, and that these actions usually do not maximize their relative fitness within the group.

Why is there usually a tradeoff? Because there is usually a tradeoff between *all* adaptations. Antipredator adaptations usually interfere with harvesting food, adaptations for moving through one medium (such as the air) usually interfere with moving through another medium (such as the water), and so on. The same principle applies to adaptations for functioning as a team player in a well-coordinated group, compared to maximizing one's relative fitness within the group. This does not mean that the tradeoff must necessarily be severe. Benefiting others or one's group as a whole does *not* invariably require extreme self-sacrifice, such as rushing into a burning house to save a child, but it *does* require some set of coordinating mechanisms, such as organizing and paying for a fire department, passing and enforcing fire safety legislation, and so on. It is unlikely that these coordination mechanisms evolve as a coincidental byproduct of organisms that are adapted exclusively to survive and reproduce better than other members of their same group. That is why Darwin felt confident in saying that "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.*" As for human morality, so also for group-level adaptations in all species.

Something more than natural selection within single groups is required to explain how altruism and other group-advantageous traits evolve by natural selection. For Darwin, in the passage quoted above, that "some-

thing" was between-group selection. Group-advantageous traits do increase the fitness of groups, relative to other groups, even if they are selectively neutral or disadvantageous within groups. Total evolutionary change in a population can be regarded as a final vector made up of two component vectors, within- and between-group selection, that often point in different directions.

The basic logic of multilevel selection applies to an enormous range of social behaviors, including the evolution of sexual reproduction and sex ratio, distastefulness in insects, prudent use of resources, warning others about predators, social insect colonies as superorganisms, and more. The relevant groupings are equally diverse, from a social insect colony (as a superorganism) or an ephemeral flock of birds (for warning calls), to multigenerational groups (for prudent use of resources), to entire species and clades (for sexual reproduction). Two related themes give these examples conceptual unity. First, single traits can evolve despite being locally disadvantageous wherever they occur. For this to happen, an advantage at a larger scale (between groups) must exist to counteract the disadvantage at a smaller scale (within groups). Second, a higher-level unit (such as a social insect colony) can become endowed with the same adaptive properties that we associate with single organisms. There can be such a thing as a superorganism. D S Wilson (1997) referred to these themes as "altruism" and "organism." They are closely related but not entirely overlapping, since becoming a superorganism involves more than the evolution of a single trait.

Evolutionary theory was placed on a mathematical foundation by the first population geneticists, in particular Ronald Fisher, Sewall Wright, and J B S Haldane. Each considered the problem of multilevel selection, but only briefly, because it was not the most important issue compared to even more foundational issues such as the consequences of Mendelian genetics (reviewed by Sober and D S Wilson 1998). All three men shared Darwin's perception that group-advantageous traits seldom maximize relative fitness within groups, thereby requiring a process of between-group selection to evolve. Unfortu-

nately, many other biologists did not share this insight and uncritically assumed that adaptations evolve at all levels of the biological hierarchy without requiring a corresponding level of selection. When the need for between-group selection was acknowledged, it was often assumed that between-group selection easily trumped within-group selection. The following passage from the textbook *Principles of Animal Ecology* (Allee et al. 1949:729) illustrates what became known in retrospect as "naïve group selectionism":

> The probability of survival of individual living things, or of populations, increases with the degree with which they harmoniously adjust themselves to each other and to their environment. This principle is basic to the concept of the balance of nature, orders the subject matter of ecology and evolution, underlies organismic and developmental biology, and is the foundation for all sociology.

Another naïve group selectionist was V C Wynne-Edwards, who proposed that organisms evolve to assess and regulate their population size to avoid overexploiting their resources in his book, *Animal Dispersion in Relation to Social Behavior* (Wynne-Edwards 1962, 1986). He was aware that group selection would be required and would often be opposed by selection within groups, but he assumed that group selection would usually prevail and proceeded to interpret a vast array of animal social behaviors according to his thesis without evaluating the levels of selection in any particular case.

These issues began to occupy center stage among evolutionary biologists in the 1960s, especially under the influence of George C Williams's (1966) *Adaptation and Natural Selection*. Williams began by *affirming* the importance of multilevel selection as a theoretical framework, agreeing with Darwin and the population geneticists that group-level adaptations require a process of group-level selection. He then made an additional claim that between-group selection is almost invariably weak compared to within-group selection (both positions are represented in the above-quoted passage). It was this additional claim

that turned multilevel selection theory into what became known as "the theory of individual selection." Ever since, students have been taught that group selection is possible in principle, but can be ignored in practice. Seemingly other oriented behaviors must be explained as forms of self-interest that do not invoke group selection, such as by helping one's own genes in the bodies of others (kin selection), or by helping others in expectation of return benefits (reciprocity). The concept of average effects in population genetics theory, which averages the fitness of alleles across all genotypic, social, and environmental contexts, was elaborated by both Williams and Richard Dawkins (1976) into the "gene's eye view" of evolution, in which everything that evolves is interpreted as a form of "genetic selfishness."

The rejection of group selection in the 1960s was based on three arguments, like the legs of a stool: a) group selection as a *significant* evolutionary force is theoretically implausible; b) there is no solid empirical evidence for group selection as a distinctive, analytically separable process; and c) alternative theories can explain the evolution of apparent altruism without invoking group selection. In the following sections, we will show that all three arguments have failed, based on subsequent research. If this information had been available to Williams and others in the 1960s, the history of sociobiology would have headed in a completely different direction. The component vectors of within- and between-group selection would need to be calculated on a case-by-case basis to determine the final vector of evolutionary change in the total population. Traits could legitimately be regarded as "for the good of the group" whenever they evolve by group selection, in the same sense that an individual-level adaptation (such as the eye) is regarded as "for the good of the individual." Instead, sociobiology proceeded along a seemingly triumphant path based entirely on the calculus of individual and genetic self-interest, under the assumption that group selection can be categorically ignored. It is precisely this branch point that must be revisited to put sociobiology back on a firm theoretical foundation.

THE THEORETICAL PLAUSIBILITY OF GROUP SELECTION AS A SIGNIFICANT EVOLUTIONARY FORCE

The rejection of group selection was based largely on theoretical plausibility arguments, which made it seem that between-group selection requires a delicate balance of parameter values to prevail against within-group selection. These early models were published at a time when the desktop computing revolution, the study of complex interactions, and appreciation of such things as social control (e.g., Ratnieks and Visscher 1989; Boyd and Richerson 1992) and gene-culture coevolution (Lumsden and E O Wilson 1981; Boyd and Richerson 1985; Richerson and Boyd 2005) were barely on the horizon. It should surprise no one that the initial assessment must be revised on the basis of four decades of subsequent research.

All of the early models assumed that altruistic and selfish behaviors are caused directly by corresponding genes, which means that the only way for groups to vary *behaviorally* is for them to vary *genetically*. Hardly anyone regards such strict genetic determinism as biologically realistic, and this was assumed in the models primarily to simplify the mathematics. Yet, when more complex genotype-phenotype relationships are built into the models, the balance between levels of selection can be easily and dramatically altered. In other words, it is possible for modest amounts of genetic variation among groups to result in substantial amounts of heritable phenotypic variation among groups (D S Wilson 2004).

The early models also assumed that variation among groups is caused primarily by sampling error, which means that it declines precipitously with the number of individuals that independently colonize each group and migration among groups during their existence. This assumption must be revised on the basis of agent-based models. When individual agents interact according to biologically plausible decision rules, a spatial patchiness emerges that has little to do with sampling error (e.g., Johnson and Boerlijst 2002; Pepper and Smuts 2002; Pepper 2007). An example is a recent simulation model on the kind of social signaling and population

regulation envisioned by Wynne-Edwards (Werfel and Bar-Yam 2004). Individuals create a local signal when crowded and curtail their reproduction accordingly. Their base reproductive rate and response to the signal are allowed to vary as independent continuous traits, including "cheaters" who reproduce at the maximum rate and ignore the signal altogether. Interactions occur on a two-dimensional lattice in which each cell represents an area occupied by the resource alone, both the resource and consumers, or by neither. Consumers that reproduce at the maximum rate are selectively advantageous within groups, but tend to drive their resource (and, therefore, themselves) extinct, exactly as envisioned by Wynne-Edwards and the early group selection models. More prudent consumers are maintained in the total population by spatial heterogeneity, which emerges spontaneously on the basis of complex interactions among the various traits. The local disadvantage of curtailed reproduction does not entirely determine the outcome of selection in the total population. In general, complex social and ecological interactions, coupled with limited dispersal, result in a kind of spatial heterogeneity that is far outside the envelope conceived by earlier models based on sampling error in the absence of complex interactions (see also Gilpin 1975; Avilés et al. 2002; Aktipis 2004).

Another early conclusion was that group selection is weak for groups that last for multiple generations, because the "generation time" is greater for groups than for individuals. Three examples will show how this conclusion has been overturned by subsequent theoretical models. First, even though altruists decline in frequency within each group and ultimately go extinct after a sufficient number of generations, the differential fitness of groups also increases with each generation, especially when the groups grow exponentially at a rate determined by the frequency of altruists. Simulations show that group selection can remain a significant force even when the groups last 10 or 15 generations between dispersal episodes (D S Wilson 1987; Avilés 1993). Second, Gilpin (1975) showed that when predator/prey dynamics are nonlinear, a small increase in predator

consumption rate can have a large effect on extinction rates, causing group selection to be effective in multiple-generation groups. Third, Peck (2004) modeled altruism and selfishness as suites of traits that must occur in the right combination to function correctly, rather than as single traits. In this case, when a selfish individual migrates into an altruistic group, its genes do not spread because they become dissociated by sexual reproduction and no longer occur in the right combination. An altruistic group can persist indefinitely, replacing less altruistic groups when they go extinct. These and other examples do not imply that group selection is *invariably* effective in multigenerational groups, but they do overturn the earlier conclusion that group selection can be categorically ignored.

Acknowledging the theoretical plausibility of group selection as a significant evolutionary force is not a return to the bad old days of naïve group selectionism. It has always been the goal of population genetics theory to provide a complete accounting system for evolutionary change, including selection, mutation, drift, and linkage disequilibrium. The question is whether group selection can be categorically ignored when natural selection is separated into within- and between-group components. Few theoretical biologists would make this claim today, however reasonable it might have appeared in the 1960s. Yet, these developments have not resulted in an appropriately revised theory, even among some of the theorists, nor have they spread to the wider community of scientists interested in the evolution of social behavior. There is a form of naïve selectionism that needs to be corrected, as before the publication of *Adaptation and Natural Selection,* but today it is the naïve assumption that group selection can be consistently ignored.

Empirical Evidence for Group Selection

The rejection of group selection in the 1960s was not based upon a distinguished body of empirical evidence. Instead, Williams (1966) used the theoretical implausibility of group selection as a significant evolutionary force to argue that hypotheses framed in

terms of individual selection are more parsimonious and, therefore, preferable to hypotheses that invoke group selection. In this fashion, broad categories of behavior such as dominance and territoriality were interpreted individualistically on the basis of plausibility arguments, without careful measurements of within- versus between-group selection for particular traits in particular species. Parsimony can be a factor in deciding between alternative hypotheses, but it cannot substitute for an evaluation of the data (Sober and D S Wilson 1998; Sober 2008). No population geneticist would argue that drift is more likely than selection and no ecologist would argue that predation is more likely than competition on the basis of parsimony. These alternatives are all plausible and their relative importance must be determined empirically on a case-by-case basis. Similarly, 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 came to a rigorous empirical test was for sex ratio, 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, as well as evidence of group selection in the evolution of disease organisms, brought him back toward multilevel selection in the 1990s (Williams and Nesse 1991; Williams 1992).

Some of the best recent evidence for group selection comes from microbial organisms, in part because they are such efficient systems for ecological and evolutionary research spanning many generations (Velicer 2003). The "wrinkly spreader (WS)" strain of *Pseudomonas fluorescens* evolves in response to anoxic conditions in unmixed liquid medium, by producing a cellulosic polymer that forms a mat on the surface. The polymer is expensive to produce, which means that nonproducing "cheaters" have the highest relative fitness within the group. As they spread, the mat deteriorates and eventually sinks to the bottom. WS is maintained in the total population by between-group selection, despite its selective disadvantage within groups, exactly as envisioned by multilevel selection theory (Rainey and Rainey 2003).

As another example, Kerr et al. (2006) created a metapopulation of bacteria (the resource) and phage (the consumer) by culturing them in 96-well microtiter plates. Migration between groups was executed by a high-throughput, liquid-handling robot according to a prespecified migration scheme. Biologically plausible migration rates enabled "prudent" phage strains to outcompete more "rapacious" strains, exactly as envisioned by Wynne-Edwards and subsequent theorists such as Gilpin (1975) and Werfel and Bar-Yam (2004). As Kerr et al. put it, "spatially restricted migration reduces the probability that phage reach fresh hosts, rendering rapacious subpopulations more prone to extinction through dilution. Consequently, the tragedy of the commons is circumvented at the metapopulation scale in the Restricted treatment" (Kerr 2006:77). More generally, the well-established fact that reduced virulence often evolves by group selection in disease organisms (Bull 1994; Frank 1996) provides a confirmation of Wynne-Edwards' hypothesis—not for *all* species, but for at least *some* species.

Multilevel selection experiments in the laboratory have been performed on organisms as diverse as microbes, plants, insects, and vertebrates (Goodnight et al. 1992; Goodnight and Stevens 1997). Phenotypic variation among groups is usually considerable, even when the groups are founded by large numbers of individuals, as expected on the basis of the newer theoretical models. For example, microcosms colonized by millions of microbes from a single well-mixed source nevertheless become variable in their phenotypic properties within a matter of days. When microcosms are selected on the basis of these properties and used to colonize a new "generation" of microcosms, there is a response to selection (Swenson et al. 2000a,b).

Quantitative genetics models separate phenotypic variation into additive and nonadditive components, with only the former leading to a response to selection (narrow-sense heritability). Laboratory selection experiments show that the nonadditive component of variation within groups can contribute to the additive component of variation among groups, causing group-level traits to be more

heritable than individual-level traits. For example, selecting plants within a single group on the basis of leaf area did not produce much response to selection, but selecting whole groups on the basis of leaf area produced a strong response to selection. This result makes sense theoretically when phenotypic traits such as leaf area are influenced by interactions among individuals within the group, rather than being directly coded by genes (Goodnight 2000, 2005).

Field studies of social vertebrates are seldom as precise as laboratory experiments but nevertheless provide convincing evidence for group selection. The following description of territorial defense in lions (Packer and Heinsohn 1996:1216; see also Heinsohn and Packer 1995) is virtually identical to Darwin's passage about human morality that began this article: "Female lions share a common resource, the territory; but only a proportion of females pay the full costs of territorial defense. If too few females accept the responsibilities of leadership, the territory will be lost. If enough females cooperate to defend the range, their territory is maintained, but their collective effort is vulnerable to abuse by their companions. Leaders do not gain 'additional benefits' from leading, but they do provide an opportunity for laggards to gain a free ride." In this field study, extensive efforts to find a within-group advantage for territorial defense failed, leaving between-group selection as the most likely—and fully plausible—alternative.

To summarize, four decades of research since the 1960s have provided ample empirical evidence for group selection, in addition to its theoretically plausibility as a significant evolutionary force.

Are There Robust Alternatives to Group Selection?

Inclusive fitness theory (also called kin selection theory), evolutionary game theory (including the concept of reciprocal altruism), and selfish gene theory were all developed explicitly as alternatives to group selection. In addition to these major theoretical frameworks, there are numerous concepts such as indirect reciprocity (Nowak and Sig-

mund 2005; Nowak 2006), byproduct mutualism (Dugatkin 2002; Sachs et al. 2004), and costly signaling (Lachmann et al. 2001; Cronk 2005) that claim to explain the evolution of cooperation and altruism without invoking group selection. Nevertheless, *all* evolutionary models of social behavior share certain key features, no matter what they are called. Recognizing the similarities can go a long way toward establishing theoretical unity for the field.

First, all models assume the existence of multiple groups. Why? Because social interactions almost invariably take place among sets of individuals that are small compared to the total population. No model can ignore this biological reality. In N-person game theory, N refers to the size of the group within which social interactions occur. In kin selection theory, r specifies that individuals are interacting with a subset of the population with whom they share a certain degree of genealogical, genetic, or phenotypic similarity (depending upon the specific formulation), and so on. The groups need not have discrete boundaries; the important feature is that social interactions are *local,* compared to the size of the total population.

Second, all models must converge on the same definition of groups for any particular trait. Why? Because all models must calculate the fitness of individuals to determine what evolves in the total population. With social behaviors, the fitness of an individual depends upon its own phenotype and the phenotypes of the others with whom it interacts. These other individuals must be appropriately specified or else the model will simply arrive at the wrong answer. If individuals interact in groups of N = 5, two-person game theory will not do. Evolutionary theories of social behavior consider many kinds of groups, but that is only because they consider many kinds of traits. For any particular trait, such as intergroup conflict in humans, mat formation in bacteria, or territorial defense in lions, there is an appropriate population structure that must conform to the biology of the situation, regardless of what the theoretical framework is called. That is the concept of the *trait-group* (D S Wilson 1975); the salient group (and

other aspects of population structure) for any particular trait.

Third, in virtually all cases, traits labeled cooperative and altruistic are selectively disadvantageous within the groups and require between-group selection to evolve. W D Hamilton (1975) realized this property of inclusive fitness theory when he encountered the work of George Price in the early 1970s (Price 1970, 1972). Price had derived an equation that partitions total gene frequency change into within and between group components. When Hamilton reformulated his theory in terms of the Price equation, he realized that altruistic traits are selectively disadvantageous within kin-groups and evolve only because kin-groups with more altruists differentially contribute to the total gene pool. Hamilton's key insight about the importance of genetic relatedness remained valid, but his previous interpretation of inclusive fitness theory *as an alternative to group selection* was wrong, as he freely acknowledged (Hamilton 1996:173–174; Schwartz 2000). The importance of genetic relatedness can be explained in terms of the parameters of multilevel selection, rather than requiring additional parameters (Michod 1982). For example, genetic relatedness might be an important factor in the evolution of territorial defense in lions, but only because it increases genetic variation among groups, thereby increasing the importance of between-group selection compared to within-group selection. Much the same conclusion has been drawn from social insects (e.g., Queller 1992; Bourke and Franks 1995; Wenseleers et al. 2003), as we will describe in more detail below.

For two-person game theory, the cooperative tit-for-tat strategy never beats its social partner; it only loses or draws. The only reason that tit-for-tat and other cooperative strategies evolve in a game theory model is because groups of cooperators contribute more to the total gene pool than groups of noncooperators, as Anatol Rapoport (1991) clearly recognized when he submitted the tit-for-tat strategy to Robert Axelrod's famous computer simulation tournament. The pairs of socially interacting individuals in two-person game theory might seem too small or ephemeral to call a group (Maynard Smith

2002), but the same dynamic applies to N-person game theory as a whole, including large and persistent groups that are described in terms of evolutionary game theory, but which overlap with traditional group selection models. All of these models obey the following simple rule, regardless of the value of N, the duration of the groups, or other aspects of population structure: *Selfishness beats altruism within single groups. Altruistic groups beat selfish groups.* The main exception to this rule involves models that result in multiple local equilibria, which are internally stable by definition. In this case, group selection can favor the local equilibria that function best at the group level, a phenomenon sometimes called "equilibrium selection" (Boyd and Richerson 1992; Samuelson 1997; Gintis 2000; the model by Peck 2004 described earlier provides an example).

Dawkins (1976, 1982) envisioned selfish gene theory and the concept of extended phenotypes as arguments against group selection but, in retrospect, they are nothing of the sort. The concept of extended phenotypes notes that genes can have effects that extend beyond the body of the individual, such as a beaver dam. Genes that cause beavers to build dams are still at a local disadvantage compared to genes in beavers in the same pond that do not build dams, so the concept of extended phenotypes does nothing to prevent the fundamental problem of social life or to provide a solution other than that provided by between-group selection. The concept of genes as "replicators" and "the fundamental unit of selection" is identical to the concept of average effects in population genetics, which averages the fitness of alleles across all genotypic, environmental, and social contexts. The average effect provides the bottom line of what evolves in the total population, the final vector that reflects the summation of all the component vectors. The whole point of multilevel selection theory is, however, to examine the *component vectors* of evolutionary change, based on the targets of selection at each biological level and, in particular, to ask whether genes can evolve on the strength of between-group selection, despite a selective disadvantage within groups. Multilevel selection models calculate the av-

erage effects of genes, just like any other population genetics model, but the final vector includes both levels of selection and, by itself, cannot possibly be used as an argument against group selection. Both Williams (1985:8) and Dawkins (1982:292–298) eventually acknowledged their error (reviewed in D S Wilson and Sober 1998; see also Okasha 2005, 2006), but it is still common to read in articles and textbooks that group selection is wrong because "the gene is the fundamental unit of selection."

A similar problem exists with evolutionary models that are not explicitly genetic, such as game theory models, which assume that the various individual strategies "breed true" in some general sense (Maynard Smith 1982; Gintis 2000). The procedure in this case is to average the fitness of the individual strategies across all of the social groupings, yielding an average fitness that is equivalent to the average effect of genes in a population genetics model. Once again, it is the final vector that is interpreted as "individual fitness" and regarded as an argument against group selection, even though the groups are clearly defined and the component vectors are there for all to see, once it is clear what to look for.

To summarize, all of the theories that were developed as alternatives to group selection assume the basic logic of multilevel selection within their own frameworks.

Pluralism

The developments outlined above have led to a situation that participants of the controversy in the 1960s would have difficulty recognizing. The theories that were originally regarded as alternatives, such that one might be right and another wrong, are now seen as equivalent in the sense that they all correctly predict what evolves in the total population. They differ, however, in how they partition selection into component vectors along the way. The frameworks are largely intertranslatable and broadly overlap in the kinds of traits and population structures that they consider. To make matters more confusing, each major framework comes in a number of varieties (e.g., Fletcher and Zwick 2006; Okasha 2006; West et al. 2007; D S Wilson 2007a). Consid-

erable sophistication is required to interpret the meanings of terms such as "altruism," "selfishness," "relatedness," and "individual selection," depending upon the specific model being employed.

This kind of pluralism is a mixed blessing. On the positive side, multiple perspectives are helpful for studying any complex problem, so long as they are properly related to each other (Sober and D S Wilson 2002; Foster 2006). On the negative side, it is easy to lose sight of the fundamental issues that made the rejection of group selection appear so important in the first place. The central issue addressed by Williams in *Adaptation and Natural Selection* was whether adaptations can evolve at the level of social groups and other higher-level units. The problem, as recognized by Darwin and affirmed by Williams, was that traits that are "for the good of the group" are usually not favored by selection within groups—what we have called the fundamental problem of social life. When Williams and others rejected group selection, they were rejecting the possibility that adaptations evolve above the level of individual organisms. This is not a matter of perspective, but a fundamental biological claim. If true, it is every bit as momentous as it appeared to be in the 1960s. If false, then its retraction is equally momentous.

A sample of issues debated by contemporary theorists and philosophers of biology will show that, whatever the merits of pluralism, they do not deny the fundamental problem of social life or provide a solution other than between-group selection. Let us begin with inclusive fitness theory. Hamilton (1963, 1964) originally interpreted the coefficient of relatedness (r), as a measure of genealogical relatedness, based on genes that are identical by descent. When he reformulated his theory in terms of the Price equation, he realized not only that kin selection is a kind of group selection, but also that r can be interpreted more broadly as any positive correlation among altruistic genes—not just based on identity by descent (Hamilton 1975). Subsequent theorists have broadened the interpretation of r still further. For example, altruistic genes can evolve as long as they associate positively with altruistic *phenotypes,* coded by the

same or different altruistic genes (Queller 1985; Fletcher and Doebeli 2006). When individuals benefit their entire group (including themselves) at their own expense, r can be positive even in randomly formed groups (Pepper 2000; Fletcher and Zwick 2004). Models that were originally conceptualized as examples of group selection, in contrast to kin selection, such as Maynard Smith's (1964) haystack model, can be reconceptualized as models of kin selection by noting that members of groups are more genetically similar to each other than to members of the total population. Generality is a virtue, so it is understandable that theorists might want to push the boundaries of inclusive fitness theory as far as possible. Nevertheless, when everything that was ever called group selection can now be described in terms of inclusive fitness theory, it is time to take stock of the original empirical issues at stake. Is the fundamental problem of social life present in the broadened form of inclusive fitness theory? Absolutely. Altruistic traits are locally disadvantageous, just as they always were. Are the ingredients of between-group selection required to solve the fundamental problem of social life? Absolutely. Altruistic traits still must be favored at a larger scale to counteract their local disadvantage. Does altruism evolve only among immediate genealogical relatives? Absolutely not. In the passage quoted at the beginning of this article, Williams (1966) rejected group-level adaptations for any groups "other than a family" or "composed of individuals that need not be closely related," by which he meant genealogical relatedness. Inclusive fitness theory refuted this claim as soon as r became generalized beyond immediate genealogical relatedness (e.g., Avilés 2002).

To pick a second example of pluralism, Kerr and Godfrey-Smith (2002a) outline two equivalent frameworks that they call *collective* and *contextual* (similar to Dugatkin and Reeve's 1994 distinction between multilevel selection and broad-sense individualism). In the collective framework, groups are assigned fitnesses and individuals are assigned different shares of their group's fitness. In the contextual framework, individuals are assigned fitnesses that are functions of the composi-

tion of their group. The distinction between the two frameworks is similar to thinking of genotypes as individuals, as in standard population genetics theory, as opposed to environments of genes, as in selfish gene theory. Kerr and Godfrey-Smith stress that the two frameworks are fully equivalent, which means that any statement in one can be translated into a statement in the other. Equivalence also means that neither is more "correct" in any causal sense, although one might provide more insight than the other in any particular case. Fair enough, but this kind of pluralism by itself does not address any particular empirical issue. When we begin to ask the empirical questions that endow the group selection controversy with such significance, we discover that the contextual approach does not avoid the fundamental problem of social life or provide a solution other than between-group selection. It merely describes these processes in different terms. In this sense "broad-based individualism" (= the contextual approach) is nothing like "the theory of individual selection" that claimed to be a genuine alternative to group selection, such that one could be right and the other wrong (for more detailed discussion of this issue, see Kerr and Godfrey Smith 2002b; Sober and Wilson 2002).

As a third example of pluralism, even though the Price equation elegantly partitions selection into within- and between-group components, it misclassifies certain cases. In particular, when individuals that differ in their individual fitness (without behaving socially at all) are separated into groups, the between-group component of the Price equation is positive, even though there is no group selection (Sober 1984). Another statistical method called contextual analysis avoids this problem, but it misclassifies other cases. Thus, there is no single statistical method that captures all aspects of multilevel selection theory (van Veelen 2005; Okasha 2006). This is interesting and important, but does not cast doubt on the basic empirical issues. In fact, the reason that we can spot classification errors in statistical methods such as the Price equation is because we have such a strong sense of what multilevel selection means in the absence of formal statistical methods.

In general, the issues discussed under the rubric of pluralism are important but also highly derived, to the point of becoming detached from the issues that endowed multilevel selection with such importance in the first place. There is a need for all perspectives to converge upon a core set of empirical claims, including the following:

1) There *is* a fundamental problem that requires a solution in order to explain the evolution of altruism and other group-level adaptations. Traits that are "for the good of the group" are seldom selectively advantageous within groups. At worst, they are highly self-sacrificial. At best, they provide public goods at little cost to the actor, making them close to selectively neutral, or they constitute a stable local equilibrium. Notice that the only way to evaluate this claim is by making a local relative fitness comparison. It is not enough to show that an individual increases its absolute fitness because it might increase the fitness of others in its own group even more (D S Wilson 2004).

2) If a trait is locally disadvantageous wherever it occurs, then the only way for it to evolve in the total population is for it to be advantageous at a larger scale. Groups whose members act "for the good of the group" must contribute more to the total gene pool than groups whose members act otherwise. This is the *only* solution to the problem from an accounting standpoint, which is why the basic logic of multilevel selection is present in all theoretical frameworks, as we showed in the previous section. In biological hierarchies that include more than two levels, the general rule is "adaptation at any level requires a process of natural selection at the same level and tends to be undermined by natural selection at lower levels." All students of evolution need to learn this rule to avoid the errors of naïve group selectionism. Notice that, so far, we are *affirming* key elements of the consensus that formed in the 1960s.

3) Higher-level selection cannot be categorically ignored as a significant evolutionary force. Instead, it must be evaluated separately and on a case-by-case basis. Furthermore, all of the generalities about the likelihood of group selection that became accepted in the 1960s need to be reexamined. Wynne-Edward's hypothesis has merit for at least some species, group selection can be significant in groups that last for multiple generations, and so on. One of the biggest problems with the current literature is that the early generalities remain unquestioned, as if there is an "old" group selection that deserves to be rejected and a "new" form that bears little relationship with its own past (e.g., Keller 1999; West et al. 2006, 2007). This is a false portrayal and cannot be justified on the basis of pluralism. Going back to basics requires acknowledgment that Williams and others were right to criticize naïve group selection, but just plain wrong in their own assessment of the likelihood of group selection. New generalities need to be formed on the basis of ongoing research.

4) The fact that a given trait evolves in the total population is not an argument against group selection. Evaluating levels of selection requires a nested series of relative fitness comparisons; between genes *within* individuals, between individuals *within* groups, between groups *within* a population of groups, and so on, each presenting traits that are separate targets for selection. All theoretical frameworks include the information for making these comparisons, as we have seen. In this sense, they are not pluralistic. They merely differ in the degree to which they focus on the comparisons on their way toward calculating evolutionary change in the total population. If we are merely interested in whether a given trait evolves, then it is not necessary to examine levels of selection, and multiple perspectives can be useful. If we want to address the particular biological issues associated with multilevel selection, then we are required to examine the appropriate information and the perspectives converge with each other.

To summarize, it is possible to acknowledge the usefulness of multiple perspectives without obscuring the fundamental biological issues that seemed so clear in the 1960s. We think that items 1–4 above can become the basis for a new consensus about when adap-

tations evolve at any given level of the biological hierarchy, restoring clarity and unity to sociobiological theory. We will now examine three cases where higher-level selection has been exceptionally important: the evolution of individual organisms, the evolution of eusociality in insects and other taxa, and human evolution.

Individuals as Groups

An important advance in evolutionary biology began with Margulis's (1970) theory of the eukaryotic cell. She proposed that eukaryotic (nucleated) cells did not evolve by small mutational steps from prokaryotic (bacterial) cells, but by symbiotic associations of bacteria becoming so integrated that the associations qualified as single organisms in their own right. The concept of groups *of* organisms turning into groups *as* organisms was then extended to other major transitions during the history of life, including the origin of life itself as groups of cooperating molecular reactions, the first cells, and multicellular organisms (e.g., Maynard Smith and Szathmáry 1995, 1999; Michod 1999; Jablonka and Lamb 2006; Michod and Herron 2006).

Despite multilevel selection theory's turbulent history for the traditional study of social behavior, it is an accepted theoretical framework for the study of major transitions. There is widespread 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 in 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. At the same time, within-group selection is never completely suppressed. There are many examples of intragenomic conflict that prevent the higher-level units from functioning as organisms in the full and truest sense of the word (Burt and Trivers 2006).

The concept of major transitions decisively refutes the notion that higher-level selection is invariably weaker than lower-level selection. The domain of multilevel selection theory has been expanded to include the internal organization of individuals in addition to the social organization of groups. Ironically, the rejection of group selection made it heresy to think about groups as like organisms, and now it has emerged that organisms are literally the groups of past ages. Okasha (2005:1008) eloquently summarizes the implications of these developments for sociobiological theory as a whole:

> Since cells and multi-celled creatures obviously have evolved, and function well as adaptive units, the efficacy of group selection cannot be denied. Just as the blanket assumption that the individual organism is the sole unit of selection is untenable from a diachronic perspective, so too is the assumption that group selection is a negligible force. For by 'frameshifting' our perspective downwards, it becomes apparent that individual organisms *are* co-operative groups, so are the *product* of group selection!

Eusociality as a Major Transition

Eusociality, found primarily in social insects but now known for other organisms such as mammals (Sherman et al. 1991) and crustacea (MacDonald et al. 2006), has always played a pivotal role in the history of sociobiology. The term "eusocial" is applied to colonies whose members are multigenerational, cooperate in brood care, and are separated into reproductive and nonreproductive castes. For the first half of the 20th century, following W M Wheeler's classic paper of 1911, eusocial colonies were treated as "superorganisms" that evolved by between-colony selection. Hamilton's (1964) inclusive fitness theory appeared to offer a very different explanation based on genetic relatedness, especially the extra-high relatedness among sisters in ants, bees, and wasps based on their haplodiploid genetic system. The focus on genetic relatedness thereafter made it appear as if social insect evolu-

tion could be explained without invoking group selection, along with other examples of apparent altruism. The following passage from West Eberhard (1981:12; parenthetical comments are hers) illustrates the degree to which between-colony selection was rejected as an explanation of eusociality in insects: "Despite the logical force of arguments against group (or colony) selection (e.g., Williams 1966) and the invention of tidy explanations for collaboration in individual terms . . . the supraorganism (colony-level selection) still haunts evolutionary discussions of insect sociality."

Four decades later, there is an urgent need to establish some fundamental biological claims that have been obscured rather than clarified by multiple perspectives. Beginning with Wheeler's original claim that eusocial colonies are superorganisms, the evolution of eusociality falls squarely within the paradigm of major transitions. Most traits associated with eusociality do not evolve by increasing in frequency within colonies, but by increasing the colony's contribution to the larger gene pool. Inclusive fitness theory is not a denial of this fact, although that is how it was originally interpreted. Hamilton's rule calculates the conditions under which an altruistic act increases the proportion of altruistic genes in the total population, not a single colony. Showing that a trait evolves in the total population is not an argument against group selection, as we have already stressed. The Price equation demonstrated to Hamilton that altruism is selectively disadvantageous within kin groups, just as in any other kind of group. The importance of kinship is that it increases genetic variation among groups, therefore the importance of between-group selection compared to within-group selection. There are traits that evolve by within-colony selection, but they are forms of cheating that tend to impair the performance of the colony, similar to intragenomic conflict within individual organisms (Ratnieks et al. 2006). All social insect biologists should be able to agree upon these facts, regardless of the theoretical framework that they employ.

Another substantive biological question is the role of genealogical relatedness in the evolution of eusociality. Hamilton's original theory was that the extra-high sociality of in-

sect colonies can be explained by the extra-high relatedness among workers, at least in haplodiploid species, when groups are founded by single queens who have mated with a single male. More generally, Hamilton's rule ($br > c$, where b = benefit to the recipient, r = coefficient of relatedness, and c = cost to the altruist) easily gives the impression that the degree of altruism should be proportional to r. This perception was in fact a principal reason for the erroneous early acceptance of collateral (indirect) kin selection as a critical force in the origin of eusociality (E O Wilson 1971, 1975).

Decades of research have led to a more complicated story in which genealogical relatedness plays at best a supporting rather than a pivotal role. The haplodiploidy hypothesis has failed on empirical grounds. In addition to termites, numerous other diploid eusocial clades in insects and other taxa have been discovered since the 1960s, enough to render the association of haplodiploidy and eusociality statistically insignificant (E O Wilson and Hölldobler 2005). Moreover, many haplodiploid colonies are founded by multiple females and/or females that mated with multiple males, lowering genetic relatedness to unexceptional levels. Further, following colony foundation in primitively eusocial wasp species, the degree of relatedness tends to fall, not rise or hold steady, at least in cases where it has been measured (e.g., Landi et al. 2003; Fanelli et al. 2004). These facts are widely acknowledged by social insect biologists but it is still common to read in the wider literature that genetic relatedness is the primary explanation for insect eusociality. In fact, extra-high relatedness within colonies may be better explained as a consequence rather than a cause of eusociality (E O Wilson and Hölldobler 2005).

From a multilevel evolutionary perspective, traits that cause an insect colony to function as an adaptive unit seldom increase in frequency within the colony and evolve only by causing the colony to out-compete other colonies and conspecific solitaires, either directly or through the differential production of reproductives. If colonies are initiated by small numbers of individuals, minimally a single female mated with a single

male, then there is ample genetic variation among groups and only modest genetic variation within groups. However, this is only one of many factors that can influence the balance between levels of selection. Consider genetic variation for traits such as nest construction, nest defense, provisioning the colony for food, or raiding other colonies. All of these activities provide public goods at private expense. All entail emergent properties based on cooperation among the colony members. Slackers are more fit than solid citizens within any single colony, but colonies with more solid citizens have the advantage at the group level. The balance between levels of selection will be influenced by the magnitude of the group-level benefits and individual-level costs, in addition to the partitioning of genetic variation within and among groups. For example, ecological constraints are more important than genetic relatedness in the evolution of eusociality in mole-rats (Burland et al. 2002). The same is true of the eusocial invertebrates (Choe and Crespi 1997; E O Wilson and Holldöbler 2005). The ancestors of most eusocial insects probably built nests and remained to feed and protect their brood throughout larval development. Such a "progressive provisioning" was evidently the key preadaptation for the origin of eusociality in the Hymenoptera. It is the multigroup population structure provided by this ecological niche and the magnitude of shared benefits that brought these species up to and over the threshold of eusociality, more than exceptional degrees of genetic relatedness.

It might seem that reproductive division of labor must be a form of high-cost altruism that requires a high degree of genetic variation among groups (represented by high r values) to evolve. This is only true, however, if heritable phenotypic variation exists for worker reproduction and if reproductive workers are not suppressed by the queen or other workers. Reproductive suppression is common in eusocial species, and to understand its evolution we need to study the policing and reproduction traits in conjunction with each other (Ratnieks et al. 2006). Suppressing the reproduction of others can be favored by within-group selection, but it can take many forms that vary in their conse-

quences for the reproductive output of the colony, compared to other colonies. Between-group selection is required to evolve forms of reproductive suppression that function well at the colony level, but the amount of genetic variation among colonies need not be exceptional. That need is diminished further when the trait favored by group selection is a form of phenotypic plasticity that enables single genotypes to be reproductive or nonreproductive—which, in fact, is universal in the social insects (E O Wilson 1975; Hölldobler and E O Wilson 1990).

In eusocial insects, it appears that the evolution of anatomically distinct worker castes represents a "point of no return" beyond which species never revert to a more primitively eusocial, presocial, or solitary condition (E O Wilson 1971; Maynard Smith and Szathmary 1995; E O Wilson and Hölldobleŕ 2005). At this point, the colony has become a stable developmental unit and its persistence depends on its ability to survive and reproduce, relative to other colonies and solitary organisms. The hypothetical mutant reproductive worker that would be favored by within-colony selection simply does not occur at significant levels or at all, although, in some species, "cheating" by workers occurs and is suppressed through policing by fellow workers. This is similar to the evolution of sexual lineages that do not give rise to asexual mutants (Nunney 1999) and the evolution of mechanisms that prevent intragenomic conflict in individual organisms (Maynard Smith and Szathmáry 1995, 1999).

A common assumption of theoretical models is that genes have additive effects on phenotypes, so that phenotypic variation among groups corresponds directly to genetic variation among groups, as we have already stressed. More complex genotype-phenotype relationships enable small genetic differences to result in large phenotypic differences, at the level of groups no less than individual organisms (D S Wilson 2004). Even a single mutant gene in a colony founded by unrelated individuals can have powerful effects on phenotypic traits such as caste development or allocation of workers to various tasks, which might provide a strong advantage to the group, compared to other groups.

Single eusocial insect colonies often have a population structure of their own, which can be spatial or based on kin recognition. There is a multiple-tiered population structure in which selection can occur between individuals within immediate families (such as matrilines or patrilines), between immediate families within a single colony, and between colonies within the larger population. In keeping with the dictum "adaptation at any level requires a process of natural selection at the same level and tends to be undermined by natural selection at lower levels," kin selection becomes part of the problem as far as colony-level selection is concerned. Numerous examples of nepotism as a disruptive force have been documented, along with mechanisms that have evolved to suppress nepotism along with individual selfishness, enabling the multifamily colony to be the primary unit of selection (Ratnieks et al. 2006; Wenseleers and Ratnieks 2006).

Social insect biologists spend much of their time studying the mechanisms that enable a colony to function as an adaptive unit. The title of one book, *The Wisdom of the Hive* (Seeley 1995), alludes effectively to Walter Cannon's (1932) *The Wisdom of the Body,* which famously described the complex physiological mechanisms of single organisms. The social interactions that enable an insect colony to make complex decisions are even directly comparable to the neuronal interactions that enable individual organisms to make decisions (Seeley and Buhrman 1999). These interactions did not evolve by within-colony selection, but by colonies with the most functional interactions out-competing other colonies. A high degree of relatedness was not required and little insight is gained by noting that individuals benefit as members of successful groups. The challenge is to understand the complex mechanisms that enable a colony to function *as a single organism,* exactly as imagined by Wheeler so long ago.

Almost all of the spectacular evolutionary efflorescence of the more than 12,000 known ant species, hence almost all the progressive advance of their communication and caste systems, life cycles, algorithms of colonial self-organization and caste-specific adaptive demographies, are manifestly the product of group selection acting on the emergent, colony-level traits, which are produced in turn by the interaction of the colony members.

We will conclude this section by discussing the extent to which pluralism has facilitated or retarded the study of the landscape of eusociality during the last four decades. The question is not whether everything that we have recounted above can be stated within the rubric of inclusive fitness theory; it can. Moreover, we certainly do not deny the advances in knowledge about social insects in recent decades, some of which has been stimulated by inclusive fitness theory as the dominant paradigm. Nevertheless, we also think that inclusive fitness theory has retarded understanding in a number of other, important respects. First, it initially gave the impression that eusociality can be explained as an individual-level adaptation, without distinguishing and invoking group (= between-colony) selection; this turned out to be a monumental mistake. Second, it misleadingly suggested that genetic relatedness is the primary factor that explains the evolution of eusociality, distracting attention from other factors of greater importance. Third, the coefficient of relatedness was originally interpreted in terms of genealogical relatedness, whereas today it is interpreted more broadly in terms of any genetic or even phenotypic correlation among group members (Fletcher et al. 2006; Fletcher and Zwick 2006; Foster et al. 2006a,b). Inclusive fitness theory now completely overlaps with multilevel selection theory, as we have already stressed. Multiple perspectives *are* useful, as long as they are properly related to each other, and we are sure that inclusive fitness theory will be used to study eusociality in the future. However, we also think that multilevel selection theory will prove to be both correct and more heuristic, because it more clearly identifies the colony as the unit of selection that has driven the evolution of the social complexity.

Human Evolution as a Major Transition

Anyone who studies humans must acknowledge our groupish nature and the importance of between-group interactions through-

out human history. Ever since the 1960s, sociobiologists and evolutionary psychologists have been burdened with the task of explaining these obvious facts without invoking group selection. In retrospect, these explanations appear needlessly contorted. Instead, human evolution falls squarely within the paradigm of major transitions (Lumsden and E O Wilson 1981; Boehm 1999; Richerson and Boyd 1999; D S Wilson 2002, 2006, 2007a,b; Hammerstein 2003; Foster and Ratnieks 2005; Bowles 2006).

A key event in early human evolution was a form of guarded egalitarianism that made it difficult for some individuals to dominate others within their own group (Bingham 1999; Boehm 1999). Suppressing fitness differences within groups made it possible for between-group selection to become a powerful evolutionary force. The psychological traits associated with human moral systems are comparable to the mechanisms that suppress selection within groups for other major transitions, such as chromosomes and the rules of meiosis within multicellular organisms and policing mechanisms within eusocial insect colonies (D S Wilson 2002; Avilés et al. 2004; Haidt 2007). The human major transition was a rare event, but once accomplished, our ability to function as team players in coordinated groups enabled our species to achieve worldwide dominance, replacing other hominids and many other species along the way. The parallels with the other major transitions are intriguing and highly instructive (E O Wilson and Hölldobler 2005).

A common scenario for human evolution begins with the evolution of sophisticated cognitive abilities, such as a "theory of mind," which in turn enabled widespread cooperation (Tomasello 1999). Now it appears more reasonable for the sequence to be reversed (Tomasello et al. 2005). Our capacities for symbolic thought and the social transmission of information are fundamentally communal activities that probably required a shift in the balance between levels of selection before they could evolve. Only when we could trust our social partners to work toward shared goals could we rely upon them to share meaningful information. The shift in the balance between levels of selection is reflected in an-

atomical features, such as the human eye as an organ of communication (Kobayashi and Kohshima 2001), and basic cognitive abilities, such as the ability to point things out to others (Tomasello et al. 2005) and to laugh in a group context (Gervais and D S Wilson 2005), in addition to more advanced cognitive and cultural activities associated with our species.

Group selection is an important force in human evolution in part because cultural processes have a way of creating phenotypic variation among groups, even when they are composed of large numbers of unrelated individuals. 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 become the most common behavior within the group and provide the decisive edge in between-group competition (Richerson and Boyd 2005). The importance of genetic and cultural group selection in human evolution enables our groupish nature to be explained at face value. Of course, within-group selection has only been suppressed, not entirely eliminated. Thus *multilevel* selection, not group selection alone, provides a comprehensive framework for understanding human sociality.

These ideas can potentially explain the broad sweep of recorded history in addition to the remote past. According to Turchin (2003, 2005), virtually all empires arose in geographical areas where major ethnic groups came into contact with each other. Intense between-group conflict acted as a crucible for the cultural evolution of extremely cooperative societies, which then expanded at the expense of less cooperative societies to become major empires. Their very success was their undoing, however, as cultural evolution within the empire led to myriad forms of exploitation, free riding, and factionalism. That is why the center of the former Roman empire (for example) is today a cultural "black hole" as far as the capacity for cooperation is concerned. Turchin, a theoretical biologist who specializes in nonlinear population dynamics, has marshaled an impressive amount of empirical evidence to support his thesis about the rise

and fall of empires as a process of multilevel cultural evolution, with profound implications for interactions among modern cultures and their consequences for human welfare in the future.

A New Consensus and Theoretical Foundation for Sociobiology

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 1960s consensus about group selection. Historians of science have made a start, including a recent article appropriately titled "The Rise, Fall, and Resurrection of Group Selection" (Borrello 2005; see also Okasha 2006), but the real need is for practicing sociobiologists to arrive at a new consensus based on the many developments that have taken place during the last four decades.

In concluding this article, it is interesting to revisit the contradictory positions that exist in the current sociobiological literature:

- Nothing has changed since the 1960s. An example is Alcock's (2005) influential textbook *Animal Behavior: An Evolutionary Approach,* in which group selection is described as non-Darwinian and a near impossibility because of the insuperable problem of selection within groups. There is no excuse for this kind of treatment, given the developments over the last four decades that we have reviewed in this article.
- Multilevel selection theory (including group selection) has been fully revived. It is important to stress once again that this is *not* a return to naïve group selectionism. On the contrary, going "back to basics" means *affirming* key elements of the consensus that formed in the 1960s, which insisted that higher-level adaptations require a process of higher-level selection and cannot be expected to evolve otherwise. The revival of multilevel selection is based solely on rejecting the em-

pirical claim that higher-level selection can be categorically ignored as an important evolutionary force. It is notable that key figures such as Williams (for sex ratio and disease virulence), Hamilton (in terms of the Price equation), and Maynard Smith (for major transitions of evolution) easily reverted back to multilevel selection when they became convinced that group selection might be a significant evolutionary force after all. It is time for everyone to follow suit, for sociobiology as a whole rather than specific subject areas.

- There is a "new" multilevel selection theory that bears little relationship to the "old" theory. According to Richard Dawkins (quoted in Dicks 2000:35) "[e]normous credit would accrue to anyone who could pull off the seemingly impossible and rehabilitate group selection . . . [b]ut actually, such rehabilitation can't be achieved, because the great heresy really is wrong." Yet, theoretical biologists widely agree that modern multilevel selection is a legitimate theory for accounting for evolutionary change. The only way to maintain these two positions is by claiming that modern multilevel selection theory bears no relationship to its own past (e.g., Keller 1999; West et al. 2006, 2007). We hope that our "back to basics" approach has established the continuity of ideas, from Darwin to the present. Moreover, other than avoiding naïve group selection, *all* of the major conclusions about group selection that seemed to emerge during the 1960s, such as the rejection of Wynne-Edward's hypothesis, need to be reconsidered on the basis of ongoing research.
- Avoiding of the topic of group selection, as if it never existed in the history of evolutionary thought. We could cite dozens of theoretical and empirical articles from the current literature that describe selection within and among groups without mentioning the term "group selection" or anything else about the group selection controversy. As one example, the microbial experiment by Kerr et al. (2006) elegantly establishes the plausibility of

Wynne-Edwards' hypothesis and describes the process matter-of-factly in terms of selection within and among groups, without citing Wynne-Edwards or the term group selection. This polite silence enables authors such as West et al. (2006) to publish tutorials on social evolution for microbiologists that portray Wynne-Edwards's hypothesis as a theoretical impossibility. This kind of pluralism is not helpful (D S Wilson 2007a). We hope that our article will help to refocus attention on the problem that has always been at the center of multi-level selection theory: the fact that group-level adaptations are seldom locally advantageous and, therefore, must be favored at a larger scale to evolve. The fact that all theoretical frameworks reflect this problem and its (partial) solution is a major simplification that should be welcomed rather than resisted.

When Rabbi Hillel was asked to explain the Torah in the time that he could stand on one foot, he famously replied: "Do not do unto others that which is repugnant to you. Everything else is commentary." Darwin's original insight and the developments reviewed in this article enable us to offer the following one-foot summary of sociobiology's new theoretical foundation: "Selfishness beats altruism within groups. Altruistic groups beat selfish groups. Everything else is commentary."

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