

Rethinking the Theoretical Foundation of Sociobiology

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One-sentence summary: Multilevel selection needs to become the theoretical foundation of sociobiology, despite the widespread rejection of group selection since the 1960s.

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Abstract

The current foundation of sociobiology is based upon the rejection of group selection in the 1960s and the acceptance thereafter of alternative theories to explain the evolution of cooperative and altruistic behaviors. These events need to be reconsidered in the light of subsequent research. Group selection has become both theoretically plausible and empirically well supported. Moreover, the so-called alternative theories include the logic of multilevel selection within their own frameworks. We review the history and conceptual basis of sociobiology to show why a new consensus regarding group selection is needed and how multilevel selection theory can provide a more solid foundation for sociobiology in the future.

Darwin identified a fundamental problem with social life in the following famous passage from *Descent of Man* (1):

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...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 realized that other-oriented behaviors are advantageous in competition with other groups, as surely as they are disadvantageous within groups.

These insights would seem to provide an excellent foundation for the study of social behavior, but that is not what happened in the history of sociobiology. Group selection—the evolutionary force that favors other-oriented behaviors according to Darwin's scenario—was widely rejected in the 1960s. Other theories, such as inclusive fitness theory (2, 3), reciprocal altruism (4), evolutionary game theory (5, 6), and selfish gene theory (7), were developed as alternatives to group selection and became the foundation for the study of social behavior in evolutionary biology.

The rejection of group selection was based on three arguments (8). First, theoretical models indicated that

between-group selection is a weak evolutionary force compared to within-group selection. Second, the empirical evidence for group selection was speculative and could just as easily be explained in terms of within-group selection. Third, the alternative theories seemed to provide more robust explanations of altruism and cooperation without invoking group selection.

Even though these arguments appeared compelling at the time, they began to be questioned as early as the 1970s. Today, after four decades of research, it has become clear that the 1960s consensus was in error. Group selection is theoretically plausible, there is solid empirical evidence for it, and the alternative theories have multilevel selection embedded within their own structures. It is difficult to revisit a major decision, but that is what must be done in the case of sociobiological theory. Here we will return to basics by reviewing the simple logic of multilevel selection, why the three arguments against group selection have failed, and how Darwin's original insight can provide a more solid foundation for sociobiological research in the future.

The Logic of Multilevel Selection. During evolution by natural selection, a trait that increases the fitness of others in a group at the expense of the individual possessing the trait will decline in frequency and ultimately will go extinct. This is the fundamental problem that Darwin identified for traits associated with human

morality, and it applies with equal force to altruistic behavior 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 traits usually do not maximize relative fitness within the group.

Something more is required to explain how other-oriented traits evolve by natural selection. For Darwin that "something" was between-group selection. Other-oriented 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.

Evolutionary theory was placed on a mathematical foundation by the first population geneticists, in particular Ronald Fisher, Sewall Wright, and J. B. S Haldane (review, 9). 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. All three writers shared Darwin's perception that other-oriented traits are usually selectively neutral or disadvantageous within groups, requiring a process of between-group selection to evolve. Unfortunately, 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. This position, which became known as "naïve group selection," was epitomized by V. C. Wynne-Edwards' *Animal Dispersion in Relation to Social Behavior* (10), which claimed that animals evolve to assess and regulate their population size to avoid overexploiting their resources.

These issues began to occupy center stage among evolutionary biologists in the 1960s, especially under the influence of George C. Williams' *Adaptation and Natural Selection* (8). 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, based on the theoretical models and empirical evidence available at the time, that between-group selection is almost invariably weak compared to within-group selection. 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 Williams and Richard Dawkins (7) into the "gene's eye view" of evolution, in which everything that evolves is interpreted as a form of "genetic selfishness."

If Williams and others had concluded in the 1960s that group selection was a significant evolutionary force, at least some of the time, then the genetic theory of sociobiology would have developed in a completely different direction. It would have become necessary to determine the component vectors of within- and between-group selection on a case-by-case basis to calculate the final vector of evolutionary change in the total population. Traits that evolve by group selection could now legitimately be regarded as "for the good of the group." Instead, a consensus formed that group selection could be categorically ignored, and as a consequence sociobiology proceeded along a seemingly triumphant path based entirely on the calculus of individual and genetic self-interest. It is precisely this branch point that must be revisited in the light of four decades of subsequent research.

The Theoretical Plausibility of Group Selection. The rejection of group selection was based largely on theoretical plausibility arguments (5, 11), 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, complexity theory, and appreciation of such things as social control (12) and cultural transmission (13, 14) were barely on the horizon. It therefore means something when group selection has become more plausible, according to more recent theoretical models.

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 today. And in fact it 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 (15).

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 completely revised in the light of complex systems theory. Complex physical systems such as the weather exhibit *sensitive dependence on initial conditions*; even tiny initial differences are magnified into larger differences by deterministic interactions. In just the same way, small initial differences among social groups caused by sampling error can be magnified by deterministic social

interactions into larger differences, upon which natural selection can act (16, 17). An example is a recent simulation model on the kind of social signaling and population regulation envisioned by Wynne-Edwards (18). 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 who 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, but 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. Selection within groups does not entirely determine the outcome of selection in the total population. In general, complex social interactions, coupled with limited dispersal, results in a kind of spatial heterogeneity that was far outside the envelope conceived by earlier models based on sampling error in the absence of complex interactions (15-23).

Acknowledging the theoretical plausibility of group selection is not a return to the bad old days of naïve group selection. It has always been the goal of population genetics 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 divided into within- and between-group components. Few theoretical biologists would make this claim today, however reasonable it might have appeared in the 1960s. Yet, the current consensus among theorists has not resulted in an appropriately revised theory, nor has it 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 has not been based upon a distinguished body of empirical evidence. Instead, Williams (8) used the theoretical implausibility of group selection 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- vs. between-group selection for particular traits in particular species. Arguments based on parsimony are weak at best and become completely invalid when alternative hypotheses are both plausible (9). 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 the 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, brought him back toward multilevel selection in the 1990s (24, 25).

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. 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 non-producing "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 (26).

Another microbial example involves the K12 strain of *E. coli*, which stops reproducing before entirely depleting its growth substrate, enabling prolonged survival under scarce resource conditions. This "prudent" strategy is vulnerable to exploitation by mutants designated by the acronym GASP (for Growth Advantage in Stationary Phase) that continue to reproduce at the expense of everyone's survival. The GASP mutant has the highest fitness within any particular group, but the "prudent" wild type is still maintained in the total population by group selection, as envisioned by Wynne-Edwards (this and other examples reviewed in 27).

Multilevel selection experiments in the laboratory have been performed on organisms as diverse as microbes, plants, insects, and vertebrates (28). Phenotypic variation among groups is usually considerable, even when the groups are founded by large numbers of individuals, as expected on the basis of sampling error magnified by complex interactions. For example, microcosms colonized by millions of microbes from a single well-mixed source nevertheless become variable in their pH or ability to degrade the toxic compound

chloroaniline within a matter of days. When microcosms are selected on the basis of these phenotypic properties and used to colonize a new "generation" of microcosms, there is a response to selection (17). Interactions that contribute to the non-additive 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 (29).

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 (30) 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 have provided ample empirical evidence for group selection, in addition to its theoretically plausibility.

Are There Robust Alternatives to Group Selection? All evolutionary theories of social behavior share a number of features, including those that were developed as alternatives to group selection. First, they all 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 relatedness, 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 genetic fitness of individuals. With social behaviors, the fitness of an individual depends upon its own phenotype and phenotypes of the others with whom it interacts. These others must be appropriately specified or else the model will simply arrive at the wrong answer. If individuals are interacting in groups of $N = 5$, 2-person

game theory won't 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* (31).

Third, in virtually all cases, traits labeled cooperative and altruistic are selectively disadvantageous within groups and require between-group selection to evolve, once the groups are appropriately identified. W.D. Hamilton (3) realized this property of inclusive fitness theory when he encountered the work of George Price in the early 1970s (32). Price had derived an equation that partitioned total gene frequency change into within and between group components. When Hamilton reformulated his theory in terms of the Price equation, he recognized 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 true, but his previous interpretation of inclusive fitness theory as an alternative to group selection was wrong, as he later acknowledged (3). The importance of genetic relatedness can be explained in terms of the parameters of multilevel

selection, rather than requiring additional parameters. 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 (33).

For 2-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 or any other cooperative strategy evolves in a game theory model is because groups of cooperators contribute more to the total gene pool than groups of non-cooperators, as Anatol Rapoport who submitted the tit-for-tat strategy to Robert Axelrod's famous computer simulation tournament, clearly recognized (review, 9). All of these models obey the following simple rule: *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" (23).

Dawkins (7) envisioned selfish gene theory as an argument against group selection but in retrospect it is nothing of the sort. 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 gives 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, however, is 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 average 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 and Dawkins eventually acknowledged their error (reviewed in 9, 34), 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 (35). 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 anyone to see, once they know what to look for.

To summarize, all of the supposed alternatives to group selection assume the existence of multiple groups and include the logic of multilevel selection within their own frameworks. Even though influential writers such as W.D. Hamilton recognized this principle as early as the 1970s, the field as a whole remained committed to the notion that group selection had been decisively rejected and replaced with robust alternatives.

Individuals As Groups. A major event in evolutionary biology occurred in the 1970s with the discovery that individual organisms are the social groups of past ages (36-38). 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, which continues for the traditional study of social behavior, it is the accepted theoretical framework for studying what has become known as major transitions in evolution. There is 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 concept of major transitions decisively refutes the notion that higher-level selection is invariably weaker than lower-level selection (34). The domain of multilevel selection theory has been vastly expanded to include the internal organization of individuals in addition to the social organization of groups.

Insect Eusociality As a Major Transition. The social insects have 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 divided into reproductive and nonreproductive castes. For the first half of the twentieth century, following W. M. Wheeler's classic paper in 1911 (39), eusocial colonies were treated as "superorganisms" that evolved by between-colony selection. Hamilton's theory of kin selection (2) 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 made it appear as if social insect

evolution could be explained without invoking group selection, along with other examples of apparent altruism.

Four decades of research has revealed the inadequacy of genetic relatedness as the primary explanation of eusociality. The haplodiploid hypothesis has failed. In addition to termites, numerous other diploid eusocial clades have been discovered since the 1960s (40). Moreover, many haplodiploid colonies are founded by multiple females and/or females that mated with multiple males, lowering genetic relatedness to unexceptional levels. Most eusocial insect colonies are genetically diverse units, just like other animal social groups, so genetic relatedness by itself cannot explain their exceptional properties. Moreover, the role of kinship has often been inflated and individual and colony-level selection erroneously rendered interchangeable, by expanding "relatedness" to include non-geneological kin and "kin selection" to include both offspring and collateral kin (41)

The paradigm of major transitions offers a more comprehensive framework for understanding the evolution of eusociality. The reason that eusocial insect colonies are so functionally organized is because group (between-colony) selection has become the dominant evolutionary force. Shifting the balance between levels of selection was a rare event, as for other major transitions. Of the approximately 2,600 living taxonomic families of insects and other arthropods, only 15 are known to contain eusocial species

(40). The advantages of group-level functional organization are so great, however, that these rare origination events gave rise to many eusocial species that comprise approximately half the biomass of all insects. The parallels with the evolution of the eukaryotic cell and multi-cellular organisms should be clear.

In the Hymenoptera at least, and likely the termites as well, the origin of eusociality is explainable not by any idiosyncrasy of genetic relatedness but as a happenstance product of ecological adaptive radiation, producing a few species in which the adults build nests and remain to feed and protect their brood through the course of larval development (37, 41). Starting with this multi-group population structure, the next step is for the offspring to remain and work altruistically in the nests, turning the groups into multigenerational units. At this point, the target of selection shifts from individual females to groups. Selection between groups favors traits, such as efficient systems of foraging and defense, that cause the colonies to function better compared to solitaires and other colonies. Selection within groups on the other hand, favors traits that claim the largest share of reproduction, even at the expense of colony function. The balance between levels of selection can be influenced by many factors, including but not restricted to genetic relatedness. Even in randomly formed groups, intense predation or competition among colonies can favor traits that help the colony as a whole to

survive, even though the traits are selectively disadvantageous to individual members of the colony.

The final step in eusocial evolution is for traits to evolve that suppress the opportunities for selection within groups, enabling between-group selection to become the primary evolutionary force. Reproductive division of labor is one effective mechanism, similar to the germ and somatic cells of multi-cellular organisms (42). Foregoing reproduction is not necessarily an act of extreme altruism; it can evolve as a form of social control enforced by policing mechanisms in groups with unexceptional degrees of relatedness. Indeed, 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. 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.

Group selection requires heritable phenotypic variation among groups, but this does not require extreme genetic variation among groups, as the theoretical and empirical studies reviewed earlier have shown. Small genetic changes can have large phenotypic effects by acting upon developmental processes, in groups no less than in single organisms. Thus, it is reasonable to expect colonies with multiple founders to vary phenotypically, providing the raw

material for colony-level selection. On the other hand, individual direct relatives (offspring) and collateral kin selection (kin other than offspring) can become a disruptive influence in colonies with multiple founders, by causing individuals to favor members of their matriline or patriline at the expense of the colony as a whole. Examples of disruptive nepotism have been documented, but they are largely suppressed by a variety of mechanisms based on group (between colony) selection similar to the suppression of individual selfishness (41).

To summarize, the eusocial insects fall squarely within the paradigm of major transitions. Heritable phenotypic variation is required for evolution at all levels. In principle, random genetic variation among groups is sufficient to evolve group-level adaptations, especially given complex genotype-phenotype relationships and strong selection pressures operating on the whole group. There is no empirical evidence or theoretical justification for supposing that genetic relatedness was a factor in the origin and elaborative evolution of eusociality. Moreover, genetic relatedness was relevant only insofar as it altered the balance between levels of selection. After 40 years of misplaced emphasis on genetic relatedness as the key factor that can explain the evolution of eusociality, it is time to return to the earlier conception of eusocial insect colonies as superorganisms that evolve by between-colony selection

following key preadaptations and key environmental selection pressures.

Human Evolution As a Major Transition. Anyone who studies humans must acknowledge our innately groupish nature and the importance of between-group interactions in human evolution. 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 (43). The psychological traits associated with moral systems can be regarded as mechanisms that suppress selection within groups, much like chromosomes and the rules of meiosis within multicellular organisms and policing mechanisms within eusocial insect colonies, enabling between-group selection to become the primarily evolutionary force (44). 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. The human major transition was a rare event, but once accomplished our ability to function as members of coordinated groups enabled us to achieve worldwide ecological dominance. The parallels with the other major transitions are intriguing and highly instructive (38).

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 (13, 43-45). The importance of 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 *multi-level* selection, not group selection alone, provides a comprehensive framework for understanding human evolution along with other major transitions.

A New Consensus and New 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 (46)," 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.

Achieving a new consensus is simpler than it might seem, once we realize that researchers for the most part have always accepted multilevel selection as a theoretical framework. There was universal agreement that group-level adaptations require a process of group-level selection and are often opposed by within-group selection. It was only the additional claim that group selection is invariably weak that turned multilevel selection theory into the theory of individual selection. Early writers such as Williams and Hamilton themselves 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 the field as a whole to follow suit. The fact that all evolutionary theories of social behavior must assume the existence of multiple groups (defined by particular traits and analyzed consistently by the logic of multilevel selection) is a major conceptual 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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