# Group Level Evolutionary Processes

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Anyone who studies human evolution, or indeed humans from any perspective, must acknowledge our groupish nature. Our environment has always been largely our *social* environment. Moreover, fitness has always been influenced by interactions among groups in addition to interactions among individuals within groups. Everyone must acknowledge these elementary facts, providing a common foundation for the study of human psychology and behavior. Unfortunately, efforts to build upon the foundation have resulted in numerous theoretical perspectives that are poorly related to each other. Our students learn about kin selection, reciprocal altruism, game theory, group selection, multilevel selection, selfish genes, byproduct mutualisms, and costly signaling as if they are separate concepts. The widespread rejection of group selection in the 1960s still casts a shadow over the entire subject. According to this consensus, groups should almost never be regarded as important units of selection. How can this belief be reconciled with the fact that groups are manifestly important in human evolution?

In short, the current literature is like the Tower of Babel, which cannot be built because so many different theoretical languages are being spoken. There is a common language that integrates all of the concepts listed above, but it requires acknowledging the importance of higher-level selection, especially in the case of human evolution. In this essay I will briefly summarize the common language of multilevel selection theory, providing references to more extensive treatments along the way.

## Natural selection is based on relative fitness

Every student of evolution learns that natural selection is based on relative fitness. It doesn't matter how well a trait enhances survival and reproduction, as long as it does so better than alternative traits. Traits that decrease absolute fitness can evolve if they decrease the fitness of everyone else even more. Traits that increase absolute fitness can fail to evolve if they increase the fitness of everyone even more. One reason that *Adaptation and Natural Selection* (Williams 1966) became a classic book is because it emphasized the importance of relative fitness and irrelevance of absolute fitness in evolutionary thinking.

## Relative fitness within and among groups

Whenever a large population is subdivided into groups, relative fitness in the total population can be divided into two components: 1) relative fitness among individuals within single groups; and 2) relative fitness among groups within the larger population (Sober and Wilson 1998). These are like vectors that can be calculated separately and then combined to yield the net direction of evolutionary change in the total population. As a classic example, consider a single group of birds that includes two types of foragers in equal proportions.  Prudent foragers restrain their feeding to manage their resources over the long term. Imprudent foragers eat and reproduce as much as possible over the short term. Imprudent foragers have the highest relative fitness and will increase in frequency within the group. The fact that the group as a whole suffers from resource overexploitation is irrelevant because natural selection is based only on relative fitness. Now suppose that there are many groups of foragers instead of just one. If the groups vary in their initial composition, then those with the most prudent foragers will persist longer and produce more dispersers, compared to groups with the most imprudent foragers. Relative fitness among groups in the total population favors the prudent foraging trait, in contrast to relative fitness among individuals within each group. Natural selection in the total population is based on the net effect of these two opposing evolutionary forces, which must be added like component vectors to produce a single final vector.

## Naïve Group Selection

Darwin thought clearly about levels of selection, especially with respect to human evolution, as indicated by numerous passages from the *Descent of Man* and elsewhere

(Borrello 2005, Richards 1987). Ronald Fisher, Sewall Wright, and J.B.S. Haldane, also thought clearly about multilevel selection, although it was not the most important thing on their minds, compared to even more foundational issues such as the consequences of Mendelian inheritance (see Sober and Wilson 1988 for more detailed discussion). Most other biologists did not share their clarity and tended to assume that adaptations evolve at all levels of the biological hierarchy, from individuals to ecosystems. This position, which is called "naïve group selection," is illustrated by the final paragraph of the textbook *Principles of Animal Ecology* (Allee et al. 1949): "The probability of survival of individual living things, or of populations, increases with the degree to which they harmoniously adjust themselves to each other and 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."

George C. Williams wrote *Adaptation and Natural Selection* to criticize this form of naïve group selection, which he encountered as a postdoctoral associate at the University of Chicago in the late 1950's (personal communication). His writing was in progress when V.C. Wynne-Edward's book *Animal Dispersion in Relation to Social Behavior* was published in 1962. Wynne-Edwards interpreted myriad social behaviors as adaptations to avoid the overexploitation of resources, similar to my example outlined above. He was aware of multilevel selection but assumed that between-group selection was sufficiently strong to oppose within-group selection, citing the work of Sewall Wright for support.

## The Rejection of Group Selection in the 1960's

Wynne-Edwards was wrong about the degree of support provided by Sewall Wright. Moreover, the issues surrounding multilevel selection only partially overlap with Wright's better known shifting balance theory. Williams was by no means the only person to criticize Wynne-Edwards and the broader tradition of naïve group selection, but his book became the most widely read analysis and the basis for a new consensus. *Adaptation and Natural Selection* is largely a tutorial on basic population genetics theory, written in non-mathematical terms for a broad biological audience (personal communication). It begins by *affirming* the importance of multilevel selection theory. Natural selection is based on relative fitness. Natural selection within groups is insensitive to the overall fitness of the group. Traits that are "for the good of the group" are usually selectively disadvantageous within groups and require a process of group-level selection to evolve. The same goes for traits that are "for the good of the species" and "for the good of the ecosystem." The general rule to keep in mind is *Adaptation at level X requires a corresponding process of natural selection at level X and tends to be undermined by selection at lower levels*.

In addition to clarifying multilevel selection theory for a broad audience, Williams also made an empirical claim that *higher-level selection is almost invariably weak compared to lower-level selection*. It is this empirical claim that turned multilevel selection into what became known as the "the theory of individual selection." Ever since, students of evolution have been taught that group selection is possible *in principle*; it just happens that it can be ignored *in practice*. Generations of students have learned about group selection with the help of a Gary Larson "Far Side" cartoon showing a group of lemmings running into the sea, supposedly to regulate their population size, except for one lemming wearing a sly smile and an inner tube (e.g., Alcock 1989). The caption in one textbook states "Gary Larson's cartoon captures the essential defect of group selection, namely, the selective advantage self-serving 'mutants' would have over self-sacrificing members of their species." Strictly speaking, this is inaccurate. It is not a *defect* that the cartoon illustrates, but rather *one vector* of multilevel selection (within-group selection) that needs to be combined with another vector (between-group selection) to see what evolves in the total population. The interpretation of the cartoon echoes G.C. Williams' conclusion that between-group selection is invariably weak compared to within-group selection. It doesn't matter that the total population includes many groups of lemmings that vary in their genetic and phenotypic composition. Everything we need to know about evolution can be determined on the strength of fitness differences within single groups.

Williams and other critics were so successful that group selection became a taboo subject in evolutionary biology, as anyone who lived through the period can attest. Every subsequent theoretical perspective, including kin selection, reciprocal altruism, game theory, and selfish gene theory, was explicitly developed as an alternative to group selection. As Richard Dawkins described his motive for writing *The Selfish Gene*, “I would write a book extolling the gene’s eye view of evolution. It should concentrate its examples on social behavior to help correct the unconscious group-selectionism that then pervaded popular Darwinism.”

## How The Consensus Collapsed

The 1960’s consensus rested upon three arguments, like the legs of a stool. The first argument was that group selection is theoretically implausible. The second argument was that no convincing empirical examples of group selection had been established. The third argument was that alternative theories (such as kin selection) do not invoke group selection in their own right. One by one, each of these arguments began to collapse, even by the early 1970’s.

With respect to theoretical plausibility, I often encounter the skeptical view that theory counts for very little in the absence of good hard evidence. However, a careful examination of the 1960’s consensus reveals that it was based almost entirely on theoretical plausibility arguments, such as Maynard Smith’s (1964) haystack model and other models reviewed in Chapter 5 of E.O. Wilson’s *Sociobiology*, which made it appear that within-group selection is invariably stronger than between-group selection. We also need to remember that the desktop computing revolution, complexity theory, and appreciation of such things as social control and cultural transmission were barely on the horizon in the 1960’s. It therefore means something when more recent theoretical models of higher-level selection have become more plausible.

With respect to empirical examples, Williams used the principle of parsimony to create a dominance hierarchy in which any argument framed in terms of individual selection, no matter how speculative, trumped any argument framed in terms of group selection. The only empirical example in *Adaptation and Natural Selection* that came close to a rigorous test involved sex ratio and led to the prediction that female-biased sex ratios would provide evidence for group selection. The subsequent discovery of many examples of female-biased sex ratio led Williams to change his mind about group selection, at least for this particular trait: “I think it is desirable…to realize that selection in female-biased Mendelian populations favors males, and that it is only the selection among such groups that can favor the female bias (Williams 1992, p. 49).” Williams also acknowledged an important role for group selection in disease evolution, as part of his more general interest in Darwinian medicine. The following passage from Williams and Nesse (1991, p. 8) shows how easily Williams reverted from individual selection back to multilevel selection, once he decided that between-group selection might be important after all: “The evolutionary outcome will depend on relative strengths of within-host and between-host competition in pathogen evolution.” Dozens of other empirical examples have emerged from field and laboratory studies, (e.g., Goodnight and Stevens 1997, Velicer 2003) making it simply false to claim categorically that group selection can be ignored as an important evolutionary force.

With respect to alternative theories, the following statements are true for virtually all models of social behavior, regardless of what they are called:

*1) Virtually all models are multi-group models*. 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.

*2) All models must converge on the same definition of groups for any particular trait*. Why? Because all models must calculate the 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 models 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 sentinel behavior, resource management, or food sharing, there is an appropriate population structure that must conform to the biology of the situation, regardless of what the model is called. That is the meaning of the term *trait-group* that I coined in 1975.

3) *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 made this discovery for inclusive fitness theory when he encountered the work of George Price in the early 1970's. 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 saw 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 intact, but his previous interpretation of inclusive fitness theory as an alternative to group selection was wrong, as he clearly acknowledged in 1975 and his autobiographical recollection (Hamilton 1996; see also Schwartz 2000). 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, the political scientist who submitted the Tit-for-tat strategy to Robert Axelrod's famous computer simulation tournament, clearly recognized (Rapoport 1991; discussed in Sober and Wilson 1998, p. 85-86). 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, which is sometimes called "equilibrium selection" (e.g., Samuelson 1997).

## The replicator concept is irrelevant to the issues associated with multilevel selection

As part of his effort to interpret basic population genetics theory for a broad audience, Williams (1966) discussed the concept of average effects, which is the fitness of alternative genes at a given locus, averaged 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. It became "the gene's eye view", "the replicator concept", and "the gene as the fundamental unit of selection" in Richard Dawkins' "selfish gene theory". These concepts were widely interpreted as arguments against group selection, but they are nothing of the sort. The whole point of multilevel selection theory is to examine the *component vectors* of evolutionary change, 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 used as an argument against group selection. Both Williams and Dawkins eventually acknowledged their error 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 (Grafen 1984). 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.

## A single theoretical framework for studying the evolution of social behavior

The collapse of all three arguments supporting the 1960's consensus requires a re-evaluation that the field as a whole has been reluctant to undertake, in part because the group selection controversy has been taught to generations of students in black-and-white terms. Once we adopt a more nuanced and historically accurate perspective, a simple solution immediately appears. Recall that Williams made two claims in *Adaptation and Natural Selection*; he *affirmed* the importance of multilevel selection as a theoretical framework and then *denied* the importance of group selection as an empirical claim. If his first claim is correct and his second claim is incorrect, then we can fix the problem by reverting back to multilevel selection theory, just as Williams did for sex ratio and disease virulence. All of the insights that we attribute to inclusive fitness theory, game theory, and other theoretical frameworks remain important, but their significance can be understood in terms of the parameters of multilevel selection theory (such as the balance between levels of selection), without requiring additional parameters. In all cases, we need to identify the appropriate groups and other aspects of population structure, examine selection differentials within groups, and then examine selection differentials among groups in the total population to determine the final vector of evolutionary change. Many evolutionists have already adopted this perspective. For them, evaluating the relative importance of within vs. between group selection has become as routine as an ecologist who evaluates the relative importance of competition vs. predation. Unfortunately, articles and books written from this matter-of-fact multilevel perspective appear alongside other articles and books that are written as if nothing has changed since the 60's, resulting in the "Tower of Babel" problem that I discussed at the beginning of this essay. A new consensus needs to be reached, or else the cynical aphorism "science progresses, funeral by funeral" will become a reality for this important subject.

## Major Transitions In Evolution

A major event in evolutionary theory occurred with the discovery that individual organisms are the social groups of past ages. Evolution proceeds not only by small mutational change, but also by groups and symbiotic communities becoming so integrated that they become higher-level organisms in their own right. Despite multilevel selection theory's turbulent history, which continues for the traditional study of social behavior, it is the accepted theoretical framework for studying major transitions. There is universal agreement that selection occurs within and among groups, that the balance between levels of selection can itself evolve, and that a major transition occurs when selection within groups is suppressed, enabling selection among groups to dominate the final vector of evolutionary change. Genetic and developmental phenomena such as chromosomes, the rules of meiosis, a single cell stage of the life cycle, the early sequestration of the germ line, and programmed death of cell lineages are interpreted as mechanisms for stabilizing the organism and preventing it from becoming a mere group of evolving elements.

Social insect colonies fall easily within the new paradigm of major transitions. Historically, social insect colonies were widely interpreted as "superorganisms" during the first half of the 20th century, only to be re-interpreted in terms of inclusive fitness theory in the 1960's. According to Hamilton (1964), the key fact about eusocial insects was the extra-high genetic relatedness among sisters in haplo-diploid species, at least if the queen has mated with only a single male. In retrospect, not only is this one factor neither necessary nor sufficient to explain the evolution of eusociality, but its limited significance can be understood in terms of the parameters of multilevel selection theory, just like all aspects of inclusive fitness theory. Genetic relatedness can even become a disruptive factor in colonies that consist of multiple matrilines and patrilines, requiring mechanisms that prevent nepotism along with individual selfishness, so that the colony as a whole can function as an adaptive unit. As Wilson and Holldobler (2005) conclude in a recent article: "Group selection is the strong binding force in eusocial evolution."

## Human Evolution As a Major Transition

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

One reason that group selection is an important force in human evolution is because cultural processes have a way of increasing phenotypic variation among groups and decreasing it within groups. If a new behavior arises by a genetic mutation, it remains at a low frequency within its group in the absence of clustering mechanisms such as associations among kin. If a new behavior arises by a cultural mutation, it can quickly becoming the most common behavior within the group. Evolutionary biologists who study cultural evolution are nearly unanimous about the importance of cultural group selection in human evolution (e.g., Gintis et al. 2005, Henrich 2003, Richerson and Boyd 2004). A recent edited volume titled *Genetic and Cultural Evolution of Cooperation* (Hammerstein 2003) shows how human cultural evolution is being studied in exactly the same way as other major evolutionary transitions.

## The Future Study of Group Level Evolutionary Processes

I began this essay by saying that anyone who studies humans must acknowledge the importance of group level evolutionary processes. Yet, a consensus formed in the 1960’s that groups are not important units of selection. Evolutionists have been struggling with this massive contradiction ever since. Some progress has been made, but much more can be made in the future by revisiting the past and forming a new consensus about the importance of higher-level selection, especially in the case of human evolution.

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