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Multilevel Selection and Major Transitions

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Multilevel selection (MLS) theory addresses a fundamental issue in evolutionary biology that was not featured strongly in the Modern Synthesis. The concept of major evolutionary transitions and human evolution as a major transition has made MLS theory more relevant than ever before. This chapter will provide a brief overview of MLS theory, major evolutionary transitions, and human evolution as a major transition, so that these subjects can become part of an extended evolutionary synthesis.

MLS Theory and Its Relation to the Modern Synthesis

Darwin's theory of natural selection is framed in terms of individual organisms surviving and reproducing better than other organisms, such as a more drought-resistant plant, a better concealed insect, a faster-running deer, and so on. These traits are *locally advantageous*; individuals possessing them are more fit than individuals in their immediate vicinity that do not.

In contrast, traits that help other organisms or that cause whole groups to function adaptively are usually not locally advantageous. Examples include helping to raise the offspring of others, watching out for predators in a way that protects everyone in the vicinity, and conserving shared resources when they are scarce. These traits are clearly "for the good of the group," but they do not give individuals possessing the trait a fitness advantage, compared with other individuals in their immediate vicinity. They are *locally disadvantageous*.

The evolution of traits that are "for the good of the group" but locally disadvantageous is not a trivial problem. Most traits associated with human morality have this "for the good of the group" quality, in addition to self-sacrificial traits in nonhuman species. Darwin proposed a straightforward solution in *Descent of Man* (1871: ch. 4) and elsewhere, as represented by this canonical passage in *Descent* (p. 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 other men of the same tribe, yet then 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. There can be no doubt that a tribe including many members who, from possessing in a high degree the spirit of patriotism, fidelity, obedience, courage, and sympathy, were always ready to aid one another, and to sacrifice themselves for the common good, would be victorious over most other tribes, and this would be natural selection. At all times throughout the world tribes have supplanted other tribes; and as morality is one important element in their success, the standard of morality and the number of well-endowed men will thus everywhere tend to rise and increase.

The human traits listed by Darwin are manifestly adaptive at the group level, despite their local disadvantage. Groups of individuals who aid each other will outcompete other groups, even if such individuals are selectively disadvantageous within groups. Natural selection can operate at more than one level of the biological hierarchy, each level favoring a different set of traits. This was the birth of what later became known as MLS theory. Darwin did not comment on the irony that morality, by this account, is primarily a within-group phenomenon and can lead to the evolution of behaviors, such as between-group conflict, that can qualify as immoral from a third-person perspective. Also, competition between groups need not take the form of direct conflict. Groups that function better as collective units for any reason will differentially contribute to the total gene pool, just as drought-resistant plants “outcompete” drought-susceptible plants in desert environments without any direct interactions.

The three fathers of population genetics theory—Ronald Fisher, J. B. S. Haldane, and Sewall Wright—all considered the problem of group-level selection, but only briefly (see Sober and Wilson 1998: ch. 1 for a review). Creating a mathematical framework for evolution in general pushed this particular problem into the shadows. Even Sewall Wright’s shifting balance theory, which bears a superficial resemblance to group-level selection, addressed the question of how individual-level traits with a complex genetic basis can evolve. When genetic interactions are epistatic, multiple local equibria exist that are not equally adaptive at the individual level, leading to Wright’s famous metaphor of a multi-peak adaptive landscape. A multigroup population structure is required for a population to inhabit more than one peak of an adaptive landscape, and there must be a way for the populations occupying the highest peaks to replace the populations occupying the lowest peaks. As strange as it might seem, Wright's first consideration of the evolution of altruistic social behaviors was a brief discussion and sketch of a model in his 1945 book review of George Gaylord Simpson's *Tempo and Mode of Evolution*. This illustrates the degree to which the issue at the heart of MLS theory was eclipsed by other issues at the heart of the Modern Synthesis.

Nevertheless, Fisher, Haldane, and Wright all confirmed Darwin's original insight, however briefly. Traits that are selectively disadvantageous within groups can evolve by causing groups to outcompete other groups. Between-group competition can take a variety of forms, such as direct conflict, fissioning at different rates, or contributing more dispersers to the total gene pool. In all cases, the local disadvantage of "for the good of the group" traits must be counterbalanced by an advantage at a larger scale for the traits to evolve in the total population.

One achievement of the Modern Synthesis of the 1940s was to make population genetics theory part of mainstream evolutionary biology. However, the problem of group-level selection remained in the shadows during the next 20 years. Moreover, many biologists did not share Darwin's original insight and naively assumed that adaptations can evolve at any level of the biological hierarchy—for the good of the individual, group, species, or even ecosystem—without requiring special conditions. When the need for higher-level selection was acknowledged, it was often assumed that it could easily prevail against lower-level selection. This position, which in retrospect is called "naive 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.

To some extent, the architects of the Modern Synthesis shared this confusion. Because evolution is a population-level process, it is easy to assume that parameters such as mutation rate, sexual reproduction, and reproductive isolation have evolved to make evolution an *efficient* population-level process. Yet, many traits, such as mutation rate and sexual reproduction, are selectively disadvantageous within populations, creating a conflict between levels of selection. These issues are still being debated under headings such as “the evolution of evolvability” (e.g., Wagner and Altenberg 1996; Pepper 2003) and “lineage selection” (e.g., Nunney 1999; Jablonski 2008), so the architects of the Modern Synthesis can be forgiven for not having fully articulated or resolved them at the time.

The problem of higher-level adaptations did not begin to occupy center stage until the 1960s, when the Modern Synthesis was firmly established. A number of authors, including most famously John Maynard Smith in England and George C. Williams in America, began to question the veracity of naive group selectionist claims. In *Adaptation and Natural Selection*, Williams (1966) interpreted population genetics theory for a broad audience of biologists, including Darwin’s original insight that group-level adaptations require a process of group-level selection and tend to be undermined by lower-level selection. Then he evaluated the evidence and made a strong claim: even though group-level adaptations can evolve in *principle*, they seldom evolve in *practice*. Higher-level selection is almost invariably weak compared with lower-level selection, and most interpretations of adaptations as “for the good of the group” are just plain wrong. As he put it (p. 93), “group-level adaptations do not, in fact, exist.”

Williams’s assessment was based less on empirical evidence than on theoretical arguments and the principle of parsimony, which dictates that simpler explanations (individual selection) be preferred over more complex explanations (group selection) whenever possible. In this fashion, broad topics such as territoriality and dominance were interpreted as individual-level adaptations based on plausibility arguments without anything close to a rigorous empirical test of selection within and among groups. The closest that Williams came to a rigorous empirical test concerned the evolution of sex ratios, in which within-group selection favors an even sex ratio and between-group selection favors either a male- or female-biased sex ratio, depending upon whether population growth or reguation is favored at the group level. Williams thought it was “abundantly clear” that most species have an even sex ratio, declaring that “I would regard the problem of sex ratio as solved” (p. 272).

Williams’s categorical rejection of group selection was widely accepted, and *Adaptation and Natural Selection* became as influential as the books associated with the Modern Synthesis published in the 1940s and 1950s.

The rejection of group selection required an explanation of seemingly other-oriented behaviors in individualistic terms. Alternatives were provided by a number of theoretical frameworks, such as kin selection theory (benefiting one's own genes in the bodies of others), reciprocity (benefiting others in expectation of return benefits), and selfish gene theory (the gene as the fundamental unit of selection for the evolution of all traits). During this period, it became almost mandatory for authors to assure their readers that group selection was not being invoked.

Ironically, group selection *was* being invoked. Almost immediately, it began to emerge that all evolutionary theories of social behavior assume the existence of multiple groups, that the traits labeled "altruistic" and "cooperative" are selectively disadvantageous within groups and require group-level selection to evolve in the total population. The various theoretical frameworks all obeyed the central logic of MLS theory and differed primarily in perspective. Several examples will be provided to illustrate the striking fact that the rejection of group selection persisted much longer than the theoretical and empirical basis for rejecting group selection.

First, one year after the publication of *Adaptation and Natural Selection*, William D. Hamilton (1967) published an influential article titled "Extraordinary Sex Ratios," which documented many examples of extreme female-biased sex ratios, especially in small species of arthropods that live in highly subdivided populations. In his mathematical model to explain the evolution of female-biased sex ratios, Hamilton assumed that a large number of groups ("hosts") are colonized at random by N individuals. In other words, the multigroup population structure could not have been more explicit. Female-biased sex ratios are selectively disadvantageous within groups but cause the group to contribute differentially to the total gene pool, exactly as Williams postulated in his use of sex ratio as an empirical test of within- versus between-group selection. Yet, aside from a footnote in which Hamilton noted the "pleasing" influence of both within- and between-group selection, he primarily described his model in terms of females maximizing their number of grand-offspring under conditions of local mate competition. This difference in perspective enabled sex ratio theory to become a hot topic in evolutionary biology without anyone noticing that it refuted Williams's best evidence against group selection, a fact that he finally acknowledged in the 1990s (Williams 1992: 49).

As a second example, Hamilton (1963, 1964) originally formulated inclusive fitness theory (termed "kin selection" by Maynard Smith 1964) as the net effect of an altruistic allele on all copies of itself identical by descent. Thus, a single altruisic act would result in a fitness decrement of c for the actor and a fitness increment of b for the recipient, which must be weighted by the probability r that the recipient possesses the same gene identical by descent. When br–c > 0, there are more copies of the altruistic allele than there were before. However, natural selection is based on relative fitness, not absolute fitness. What if the altruistic act increases the number of nonaltruistic genes in the vicinity even more? In the early 1970s, Hamilton reformulated his theory on the basis of an equation derived by George Price (1970, 1972) that is more explicit about the fact that social interactions among relatives inherently imply a multigroup population structure. When it was viewed through the lens of the Price equation, Hamilton immediately saw that altruism expressed among relatives is locally disadvantageous, just as any other form of altruism, and evolves only by virtue of groups of altruists differentially contributing to the total gene pool. High degrees of genetic relatedness signify high genetic variation among groups, increasing the importance of between-group selection compared to within-group selection. Hamilton's theory remained a powerful explanation for the evolution of altruism, but emerged as a *kind of* group selection rather than *an alternative* to group selection, as he clearly acknowleged in 1975. Yet, Hamilton's new formulation did not cause the field as a whole to reconsider the rejection of group selection that was now in full swing.

As a third example, game theory became a popular theoretical framework for studying the evolution of cooperation and altruism in the 1980s (e.g., Axelrod and Hamilton 1981; Maynard Smith 1982). As with inclusive fitness theory, game theorists did not think that they were invoking group selection. The core game theory models assume pairwise interactions, but two-person game theory easily generalizes to n-person game theory, where n refers to the groups of individuals that actually interact and determine each other's fitness. In other words, evolutionary game theory models assume a multigroup population structure, just like all other models of social behavior. The groups can form at random, as groups of relatives, or by other processes such as assortative interactions. Traits labeled "cooperative" and "altruistic" are selectively disadvantageous or at best neutral within groups, and evolve only by virtue of the differential contributions of groups to the total gene pool. One reason that the central logic of MLS theory is not more obvious in game theory models is because the fitness of individual strategies is averaged across groups rather than partitioned into within- and between-group components. Thus, a conditional strategy such as tit-for-tat can evolve in the total population, even though individuals employing the tit-for-tat strategy never beat their social partners in within-group social interactions. It is very easy to label the strategy that evolves in the total population "individually advantageous" without checking to see the scale (within-group versus between-group) at which the advantage resides.

As a fourth example, Williams (1966) discussed the concept of average effects as part of his exposition of population genetics theory. The average effect of a gene is its fitness averaged across all genotypic and social contexts, and provides the "bottom line" of what evolves in the total population. Williams accurately called it a "bookkeeping method." As such, it includes group selection as an evolutionary force, no matter how weak or strong. A gene coding for altruism that evolves by group selection, despite its selective disadvantage within groups, has a higher average effect than the alternative gene for selfishness, which is just another way of saying that it evolves. Nevertheless, the concept of average effects soon began to be interpreted as an argument against group selection. Genes were called "the fundamental unit of selection," and all genes that evolve were termed "selfish genes" (Dawkins 1976). Only in retrospect has it become obvious that the "replicator" concept is no argument at all against group selection. Similarly, the concept of extended phenotypes (Dawkins 1982) notes that genes can have effects that extend beyond the body of the individual containing the gene. True enough, but this fact by itself says nothing about the fundamental issue that MLS theory was designed to solve—the fact that some genes are locally disadvantageous and can evolve only by being advantageous at a larger scale.

To summarize, what was originally a strong empirical claim—lower-level selection invariably trumping higher-level selection—has been authoritatively rejected. In its place, we have a collection of theoretical frameworks that all assume the existence of multiple groups and the central logic of MLS, but that differ in how they calculate the bottom line of what evolves in the total population. The coexistence of multiple equivalent theoretical frameworks is called pluralism (D. S. Wilson 2008; D. S. Wilson and E. O. Wilson 2007). Today, a pluralistic scientist might prefer inclusive fitness theory for its heuristic value, but would cheerfully acknowledge that altruism is selectively disadvantageous within groups and requires group selection, as these terms are used in MLS theory. Pluralism has its merits, but it sometimes obscures how much has changed since the rejection of group selection in the 1960s. Darwin was right:

traits can evolve by virtue of benefiting whole groups, despite being selectively disadvantageous within groups. Within-group selection does not invariably trump between-group selection, and their relative importance must be determined on a case-by-case basis. (See Sober and Wilson 1998 for a review of the turbulent history of group selection, and Okasha 2007, and D. S. Wilson and E. O. Wilson 2007, 2008 for more detailed reviews of contemporary MLS theory.)

How does MLS theory relate to the modern synthesis? It falls squarely within the paradigm of microevolution, population genetics models, and an emphasis on adaptation and natural selection established by the Modern Synthesis. However, the central focus of MLS theory—whether "for the good of the group" traits can evolve—didn't occupy center stage until the 1960s, 20 years after the Modern Synthesis had become established. MLS theory can therefore be truly regarded as an *extension* of the Modern Synthesis. The fact that *Adaptation and Natural Selection* became as influential as the books associated with the Modern Synthesis illustrates that MLS theory is an *important* extension. Finally, the revival of MLS theory shows that it *continues* to be an important extension in contemporary research.

Major Evolutionary Transitions

The balance between levels of selection is not static, but can itself evolve. When between-group selection sufficiently dominates within-group selection, the group becomes so functionally organized that it becomes a higher-level organism in its own right.

This scenario was proposed by the cell biologist Lynn Margulis (1970) to explain the evolution of the eukaryotic cell not by small mutational steps from bacterial cells, but as symbiotic associates of bacteria. Few biologists noticed that Margulis's theory, which involves between-group selection trumping within-group selection, was diametrically opposed to the dogma that within-group selection invariably trumps between-group selection.

Later, John Maynard Smith and Eörs Szathmáry (1995, 1999) expanded Margulis's theory to include other major transitions in the history of life, including the origin of life itself, as groups of cooperating molecular reactions, the first cells, multicellular organisms, social insect colonies, and human evolution. In each case, mechanisms evolve that suppress selection within groups, causing between-group selection to become the dominant evolutionary force.

A major transition includes a number of hallmarks: (1) It is a rare event; (2) It results in momentous consequences once it occurs—lower-level organisms are no match for the new superorganism, which becomes ecologically dominant and radiates through evolutionary time to become thousands of species; (3) The transition is never complete—within-group selection is only suppressed, not entirely eliminated. Even multicellular organisms have a disturbing number of genetic elements that spread by intragenomic conflict rather than "for the good of the group" (Burt and Trivers 2006).

The concept of major evolutionary transitions is one of the most important developments in evolutionary biology. The architects of the Modern Synthesis imagined all evolution to be the result of small mutational steps—individuals from individuals. The concept of major transitions identifies an entirely new pathway—individuals from groups. Although major transitions fall squarely within MLS theory, they were not predicted by MLS theorists prior to Margulis's bold symbiotic cell theory. These foundational developments have surely gone beyond the Modern Synthesis.

Human Evolution as a Major Transition

Although Maynard Smith and Szathmáry (1995, 1999) were bold about expanding the concept of major transitions, they were timid about applying it to human evolution, restricting themselves to a discussion of the genetic basis of language, which by itself does not obviously relate to major transitions. Now it appears likely that human evolution was a full-fledged major transition, from groups *of* organisms to groups *as* organisms. The reason that we are so unique among primates is that our ancestors became the primate equivalent of a single organism or a social insect colony (Boehm 1999; D. S. Wilson 2007; Wilson, Van Vugt, and O'Gorman 2008).

Recall that the key ingredient of a major transition is the suppression of fitness differences within groups, causing between-group selection to become the primary evolutionary force. In most primate species, including our closest ancestors, intense within-group competition limits the opportunities for cooperation among members of the group. This is in contrast to extant human hunter-gatherer societies, which are fiercely egalitarian. What accounts for this shift, and when did it occur in human evolution?

Humans are incomparably better at throwing projectiles than other primates are, an ability that required whole-body anatomical changes and evolved early in the hominid lineage. Although the original purpose of throwing was presumably to deter predators and competing scavengers, it could also be used to suppress bullying and other domineering behavior within groups (Bingham 1999). This is a specific version of a more general hypothesis of guarded egalitarianism, originally advanced by Boehm (1993, 1999) on the basis of the egalitarian nature of most extant hunter-gatherer societies. However it was accomplished, guarded egalitarianism provides the key ingredient of an evolutionary transition.

It has been common in the past to regard advanced human cognitive abilities, such as a theory of mind, as the first step of human evolution that made widespread cooperation possible (e.g., Tomasello 1999). Now it appears that the sequence needs to be reversed (e.g., Tomasello et al. 2005). The first event was the suppression of fitness differences within groups, based upon adaptations such as the ability to throw stones, which did not require a change in social cognition. Then, between-group selection favored forms of mental cooperation in addition to physical cooperation. After all, symbolic thought and the social transmission of behaviors are fundamentally cooperative activities that are unlikely to take place among uncooperative individuals. Even human capacities that we take for granted, such as the communicative nature of our eyes, our ability to point, and awareness of others that emerges early in infancy, are forms of cooperation that appear to be uniquely human (reviewed by Tomasello et al. 2005).

In retrospect, human evolution has all the hallmarks of a major transition. It was a rare event, occurring only once among primates. It had momentous consequences; cooperation enabled our ancestors to spread over the planet, eliminating other hominids and many other species along the way. We also diversified to occupy all climatic zones and hundreds of ecological niches, although by cultural evolution rather than genetic evolution. The advent of agriculture enabled us to increase the scale of society by many orders of magnitude through a process of cultural multilevel selection (e.g., Turchin 2005). Finally, the transition was not complete. Within-group selection still takes place, and is merely suppressed compared with between-group selection.

Thinking of human evolution as a major evolutionary transition is so new that most of the implications remain to be discovered, providing yet another area of study that was not anticipated by the Modern Synthesis.

A Postscript on the Study of Human Behavior and Culture from an Evolutionary Perspective

This chapter is mostly about MLS, but I would like to end with a comment on all aspects of human behavior and culture from an evolutionary perspective. It was obvious to everyone in Darwin's time that, if true, his theory would revolutionize our understanding of ourselves. Yet, by the early twentieth century, studying human behavior and culture from an evolutionary perspective was largely off-limits. The Modern Synthesis respected this boundary for the most part, saying much about biology but remaining cautious about human behavior and culture. In his book *Mankind Evolving*, for example, Dobzhanksy (1962: 345) stated that "I know no better criterion of wisdom and values" than the following passage from an ancient Chinese sage:

> Every system of moral laws must be based upon the man's own consciousness, verified by the common experience of mankind, tested by due sanction of historical experience and found without error, applied to the operations and processes of nature in the physical universe and found to be without contradiction, laid before the gods without question or fear, and able to wait a hundred generations and have it confirmed without a doubt by a Sage of posterity.

This passage might be edifying, but it is difficult to know what it has to do with evolution in any concrete sense.

In 1973, Dobzhansky made his oft-quoted statement "Nothing in biology makes sense except in the light of evolution." Two years later, E. O. Wilson (1975) provided an example in the form of *Sociobiology: The New Synthesis*, which claimed that the social behavior of all species, from ants to primates, could be understood on the basis of the same evolutionary principles. Sociobiology was celebrated as a major advance—except for the last chapter on humans, which ignited a storm of controversy. Wilson was attempting to relate evolutionary theory to human behavior in a much more concrete sense than Dobzhansky in *Mankind Evolving*, but this was not admissible in 1975.

It wasn't until the 1990s that terms such as "evolutionary psychology" and "evolutionary anthropology" began to gain currency, and even then they had the air of scandal about them. In short, although evolutionary biology developed into an enormously sophisticated science during the twentieth century, its widespread application to human behavior and culture has only taken place only since the mid-1990s. If the theme of the present volume is how evolutionary theory has gone beyond the

Modern Synthesis, then the inclusion of human behavior and culture counts as one of the most important recent extensions, including but not restricted to the concept of human evolution as a major evolutionary transition.

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