# Reaching a New Plateau for the Acceptance of Multilevel Selection

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"Chapters 5 to 8 [of *Adaptation and Natural Selection*] will be primarily a defense of the thesis that group-related adaptations do not, in fact, exist. "
--G.C. Williams (1966 p. 93)

"In earlier debates, biologists tended to regard kin and multilevel selection as rival empirical hypotheses, but many contemporary biologists regard them as ultimately equivalent, on the grounds that gene frequency change can be correctly computed using either approach. Although dissenters from this equivalence claim can be found, the majority of social evolutionists appear to endorse it"
--J. Birch and S. Okasha (2014 p. 28)

There can be no doubt, for anyone who reads the academic literature on the subject, that Multilevel Selection (MLS) theory has reached a plateau of acceptance far above its almost complete rejection in the 1960s. Back then, it was almost mandatory for authors studying social evolution to state that their model or empirical study did not invoke group selection, relying instead upon kin selection (=inclusive fitness theory), reciprocity (=evolutionary game theory), or selfish gene theory. Now it has become almost mandatory to write something similar to the passage from Birch and Okasha (2014), acknowledging that the theories that seemed to replace group selection in fact only offered different ways of accounting for the same causal processes, a concept that has become known as equivalence (Okasha 2006, Wilson 2015a).

MLS theory has become especially prominent for the study of human cultural evolution, where it can even be regarded as the theory of choice (Boyd and Richerson 1985; Richerson and Boyd 2006; Henrich 2015). Processes such as conformance transmission and especially the formation and enforcement of norms can create extreme phenotypic differences among groups and uniformity within groups—the raw material upon which multi-level selection acts. Warfare can cause even small phenotypic differences among groups to result in large differences in survival and reproduction (the victor and defeated; Bowles 2009). Finally, the concept of equivalence, which applies to the core genetic models of social evolution, might not always extend to human cultural evolution. In other words, MLS might be not just one of several ways to account for human cultural evolution, but the only feasible way (Wilson 2015b). Turchin (2015) expressed this view when he wrote "The central theoretical breakthrough in this new field is the theory of Cultural Multilevel Selection."

Despite these gains, the purpose of this essay is to show that a new plateau of acceptance is needed for MLS Theory. Progress needs to be made along the following fronts.

- There is a disconnect between the peer-reviewed academic literature and the popular literature, including the blogosphere, where MLS is often still portrayed as a failed theory.

- There are still a few doubters among respected and qualified scientists, notably Steven Pinker, whose essay titled "The False Allure of Group Selection", published on the online magazine Edge.org, is widely cited as proof that the 1960's consensus still holds.

- There is a disconnect between those who study human cultural MLS and those who study genetic MLS, leading to a widespread attitude among the former that group selection is only strong in the case of cultural evolution and that the1960's consensus remains valid for genetic MLS.

- The concept of equivalence needs to be refined. Establishing that the major theories of social evolution are inter-translatable was an important step toward the revival of MLS theory but might only apply to a core set of models with simplifying assumptions such as additive genetic interactions. As the models become more complex, an argument can be made that MLS becomes the theory of choice—for genetic in addition to cultural evolution--and that alternative accounting methods become unwieldy or impossible. Thus, part of the new plateau is to establish the concept of *partial equivalence*.

I have been meaning to write an essay such as this for a long time but was moved to act by a debate between Joseph Henrich and Max Krasnow, moderated by Richard Wrangham at Harvard University, which can be viewed on You Tube (https://www.youtube.com/watch?v=kmpSwbtWopM). It was sponsored by the Mind, Brain and Behavior Graduate Student Steering Committee and titled "Culture, Evolution, and the Human Mind." One could not ask for a more elite academic event. Nevertheless, all of the problems listed above that require a new plateau for the acceptance of MLS were on display. The debate therefore provides a teachable moment and I refer to it repeatedly in my essay, including passages that are marked by where they occurred during the debate for easy reference.

I have chosen the online magazine *This View of Life* as the venue for this target essay and commentaries to reach a large audience that includes specialists and the general public. I have written the essay to be accessible to non-specialists but otherwise have abided by and expect to be held accountable to the standards of the peer-reviewed literature.

One final caveat before proceeding: It might seem awkward to criticize colleagues who are highly respected in their fields for various misunderstandings about MLS theory, which requires an essay such as this to remedy. However, the problems that I am trying to address are systemic and not a matter of individual culpability, caused in large part by the extreme interdisciplinarity that is called for and has not yet been achieved. It makes a difference that Henrich, Krasnow, and Wrangham are trained in cultural evolutionary theory, evolutionary psychology, and anthropology respectively, while my own training is in general evolutionary theory. Science is a process of constructive disagreement and I have the highest respect for the colleagues whose views I will be critiquing.

## The basic Tenets of MLS Theory

The basic tenants of MLS theory are easy to state in words without requiring mathematical equations (see Wilson 2015 for a concise book-length account).

1) Natural selection is based on relative fitness. It doesn't matter how well an organism survives and reproduces in absolute terms; only that it does so better than other organisms in its vicinity.

2) Social behaviors are almost invariably expressed among sets of individuals (groups) that are small compared to the total evolving population. Thus, almost all evolving populations are *multi-group* populations. The groups form, dissolve, and are connected to each other in diverse ways, depending upon the species, which is collectively referred to as the *population structure*.

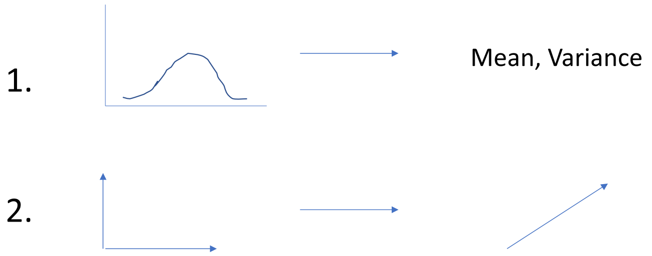
3) Natural selection among individuals within any given group tends to favor self-serving behaviors such as free-riding and active exploitation in all their forms, which increase in frequency compared to group-serving behaviors such as altruism and the provision of public goods for the whole group. This is a basic matter of trade-offs. Behaving for "the good of the group" requires members to spend time, energy, and risk on each other's behalf, which lowers fitness within the group compared to members who don't perform the services. Even the provision of a no-cost public good is merely neutral as far as within-group selection is concerned. There are no fitness differences in a win-win situation.

4) If group-serving behaviors don't evolve (and are frequently opposed) by within-group selection, then they must evolve by between-group selection; in other words, the differential contribution of groups to the total evolving population. As Edward O. Wilson and I put it in the conclusion to our 2007 article "Rethinking the Theoretical Foundation of Sociobiology": Selfishness beats altruism within groups, altruistic groups beat selfish groups, and everything else is commentary.

Even if the reader knows nothing more about MLS theory than these basic tenets, they are sufficient to make my points about the need to reach a new plateau of acceptance.

## Equivalence and the Averaging Fallacy

To understand the concept of equivalence, consider the first two examples in figure 1. A frequency distribution can be summarized as a mean and variance and two component vectors can be summarized as a resultant vector. In both cases there is a loss of information. There is no way to recreate a distribution from its mean and variance and no way to recreate component vectors from a resultant vector.



3. $\Delta p$(within) + $\Delta p$(between) = $\Delta p$(total)

Figure 1. Three examples of summary statistics that result in a loss of information

In the third example of figure 1, gene frequency change within and between groups can be used to calculate the net change in the total population. As with the other two examples, there is a loss of information. If all we know is that the frequency of the gene changes from 0.10 to 0.12 in the total population, this can be due to any combination of within- and between-group selection that results in an increment of 0.2. Knowing only what evolves in the total population does not provide sufficient information to evaluate the contribution of within and between group selection. To use the fact that a behavior evolves in the total population as an argument against group selection is to commit a fallacy that Elliot Sober and I called the Averaging Fallacy over 20 years ago (Wilson and Sober 1994; Sober and Wilson 1998).

While the Averaging Fallacy might seem obvious once pointed out, this is only in retrospect. W.D. Hamilton, the originator of kin selection theory, discovered that he had committed the Averaging Fallacy through the work of another theoretical biologist named George Price, a story well told by the historian of science Oren Harman (2010). Price had derived an equation that statistically partitioned selection in the total population into within- and between-group components, much like the third example in Figure 1. When Hamilton looked at his own theory through the lens of the Price equation, he discovered that selfishness beats altruism within kin groups, just like any other kind of group, and evolves only because kin groups with more altruists contribute more to the total population than kin groups with fewer altruists. The importance of relatedness for the evolution of altruism was to segregate the altruists and selfish individuals into separate groups. This did not make Hamilton's original formulation wrong or un-useful. The only thing that Hamilton originally got wrong was to regard his theory as an alternative to group selection, a fact that he was happy to acknowledge in an article published in 1975, over forty years ago.

The same story can be told for evolutionary game theory and selfish gene theory. The term N in N-person game theory defines the number of individuals that are socially interacting with each other. It is easy to confirm that the strategies labeled cooperative and altruistic are selectively disadvantageous in these groups and evolve only by virtue of the differential contribution of the groups to the total population. All of the tenets of MLS theory listed earlier are included in evolutionary game theory. However, this fact is obscured when the fitness of each strategy is averaged across groups and the most fit strategy, all things considered, is called a product of individual-level selection. Likewise, gene selfishness is defined in terms of the fitness of genes averaged across all genotypic and social contexts. None of these frameworks are wrong or un-useful when it comes to describing what evolves in the total population—only when described as an alternative to group selection.

Decades were required for the concept of equivalence to become the consensus view among social evolutionists, no matter what their preferred framework, which is reflected in the passage by Birch and Okasha (2014) quoted at the beginning of this essay. Nevertheless, much of the Harvard debate can be seen as Henrich operating on the left side of the equation in figure 1, partitioning selection into within- and between-group components, and Krasnow and Wrangham operating on the right side of the equation, defining their terms on the basis of what evolves in the whole population. For example, Wrangham humorously begins the debate by reporting his effort to prepare for his role as moderator by asking Henrich and Krasnow to articulate their differences (1:03).

> *"It got me to the point of saying 'Are there any differences at all?' Because every time we started thinking about the fact that culture is the result of psychological mechanisms that have been selected through genetic processes, I would say 'Are we agreed upon that? Are we disagreed upon that?' and it turns out that we're all agreed upon that."*

Wrangham is thinking only about what evolved by genetic processes in the whole human population—the right side of the equation in figure 1. It doesn't occur to him that the main issue dividing Henrich and Krasnow might concern whether the genetic processes take the form of within-group vs. between-group selection—the left side of the equation in figure 1.

Henrich includes an extended example of cultural group selection in his presentation (starting at 11:30). In a region of New Guinea, most villages have a maximum of 300 people with the exception of one that is five times larger, making it dominant in between-group competition. This village owes its large size to a novel religion, whose beliefs and ritual practices keep the villagers interacting at a larger scale than they would otherwise. There is no evidence that the villagers designed their religion with enhancing group size in mind. If that were the case, then every village would have done the same. Instead, the new religion came together in a haphazard fashion, like a random mutation that just happened to have the effect of increasing group size. Presumably, assuming that the new religion proves sufficiently stable, it is likely to spread in competition with smaller groups.

The new religion had already spread by within-group selection in its natal group, but so also had the religions of the other villages. This is an example of what is called equilibrium selection (Samuelson 1997). Social interactions result in multiple stable local equilibria that differ in their group-level properties. Group selection therefore takes the form of selection among local equilibria rather than selecting for altruistic traits that are selectively disadvantageous within groups. Equilibrium selection is especially important in human cultural evolution because norms can stabilize any suite of behaviors, as Henrich states at 21:52.

An example of equilibrium selection that has already largely run its course is norms that favor monogamous marriage (MacDonald 1995; Henrich et al. 2012). Men within any society have powerful incentives to marry more than one woman and women have incentives to enter into a polygamous marriage with powerful men rather than a monogamous marriage with less powerful men. However, polygamous societies tend to be unstable because of the large numbers of men without reproductive prospects. Monogamous societies therefore tend to beat polygamous societies in between-group competition, a fact that can be documented in the historical record.

These examples demonstrate the logic of multilevel selection for culturally evolved traits. Henrich is clearly operating on the left side of the equation in Figure 1, examining the relative contributions of within- and between-group selection on his way toward explaining what evolves in the total population.

The next teachable moment comes when Henrich describes a recent article by Krasnow on third party punishment, a topic that Henrich has also published on (starting at 23:39). Third-party punishment involves the co-evolution of two traits, cooperate vs. cheat and punish vs. don't punish. If punishers are sufficiently frequent in a social group, then cooperators are more fit than cheaters and evolve by within-group selection.  However, punishers are always less fit than non-punishers within the same group because they are providing a public good at some cost to themselves. Thus, between-group selection is required to explain the evolution of the punishment behavior, which is why it is often termed altruistic punishment (Fehr and Gachter 2002). Krasnow's alternative explanation is that third-party punishment is "the psychology of deterrence for defending personal interest."

Whatever Krasnow means by personal interest, it is not the fitness of punishers compared to non-punishers within the same group. By failing to take note of fitness differences within groups, Krasnow loses the ability to evaluate whether this trait evolves by within- vs. between-group selection. When he claims that punishment is self-interested just because it evolves in the total population, he is committing the Averaging Fallacy.

Krasnow demonstrates the same style of reasoning again and again during his presentation. Here is his articulation of what he calls "the strong EP view" that starts at 41:40.

> *"On this view, many of the mechanisms that underlie our sociality are going to have long histories into our deep ancestry, that well predates the modern cultures of the last tens of thousands of years. These mechanisms are going to be myriad. Mechanisms of social change, partner choice, personal bargaining and conflict management, social learning, mate choice, coalition management, foraging—on and on and on. Many of these mechanisms evolved over regularly variable conditions, so they should in fact be designed to be calibrated by local physiological, social, and informational conditions. Because of what some of these mechanisms calibrate to, is in fact the very social environment that they shape for action, the output in the sense of your mechanism becomes the input to mine. That's what can calibrate my mechanism over time. Linking these processes together, and giving them time to feed back on each other directly predicts both changes in a culture over time and regional variation in cultural forms."*

Like Wrangham's introduction to the debate, this broad brush portrayal only describes what evolves by genetic processes over immense periods of time. There is no attempt to outline the population structure for any particular trait, much less delineate relative fitness differences within and between groups. By operating entirely on the right side of the equation in figure 1, Krasnow has lost the ability to identify group selection when it exists. In his mind, however, all of it is "personal interest" because it evolved in the total population. Individuals constructed that way were more fit than individuals constructed other ways, all things considered. This is the Averaging Fallacy, pure and simple. Henrich makes some of these points himself without alluding to the Averaging Fallacy per se. For example, at 1:03:03 he states: "I see a list of claims about cognitive adaptations that humans have, but I don't see a detailed description of the evolutionary process that brought them into existence."

To summarize, there is no way to comment on either genetic or cultural group selection without identifying the population structure for the trait(s) under consideration and examining relative fitness differences within and between groups. Defining what evolves in the total population as "individual selection" and using this to argue against group selection is a fallacy that W.D. Hamilton identified almost fifty years ago and Elliott Sober and I called attention to over 20 years ago. It is now avoided by most evolutionary biologists, as represented by the passage by Birch and Okasha (2014) quoted at the beginning of this essay. Yet, it still pervades "the strong EP view" as represented by Krasnow. Much of Pinker's critique of group selection in his Edge.org essay commits the same fallacy. Only when Evolutionary Psychologists move over to the left side of the equation in Figure 1 will they be able to say anything about cultural or genetic group selection.

## Genetic Group Selection

For me, the most discouraging moment of the debate occurred when Wrangham stated (1:08:48): "I think that neither of you want to advocate for genetic group selection" and neither Henrich nor Krakow disagreed. The idea that the widespread rejection of group selection remains valid for genetic evolution and only needs to be revised for cultural evolution is common among those whose interest is centered on human evolution and are perhaps unfamiliar with the rest of the biological literature. This is regrettable, because genetic group selection is required even to explain the case of human evolution.

The following points about genetic group selection are widely accepted in the biological literature. To say that the 1960's consensus against genetic group selection remains valid ignores the concept of equivalence covered in the previous section. At the very least, the role of between-group selection for examples of altruism and cooperation already accepted under the labels of the other theoretical frameworks needs to be acknowledged.

In addition, much of the reasoning that made group selection appear implausible in the 1960s has proven to be erroneous, often based on simplifying assumptions required to make the theoretical models tractable at a time when desktop computing and computer simulation models were in their infancy. One of the most influential early models demonstrating the implausibility of group selection assumed (to simplify the math) that altruists go extinct in every group colonized by one or more selfish individuals before dispersal from the group takes place (Maynard Smith 1964). A later computer simulation model made the more reasonable assumption that while the altruistic trait declines in frequency within every group containing both types, it does not necessarily go entirely extinct before dispersal takes place. Altruism robustly evolved in this model (Wilson 1987).

To give a second example, consider a multi-group population in which every group is colonized at random by N individuals and a certain proportion (m) randomly migrates between groups every generation. N and m must be small to maintain genetic variation among groups, which seems restrictive. Now consider a more complex and biologically reasonable model where the decision to leave a group is based on the proportion of altruists in the group. In these so-called "walk-away" models, dispersal can *increase* variation among groups rather than eroding it (Aktipis 2004). At one point in Henrich's presentation (22:20), he lists conditional movement as an important factor in human cultural group selection, but conditional movement has nothing to do with culture and doesn't require sophisticated cognitive abilities. In a series of empirical studies, Eldakar et al. (2009a,b) demonstrated a walk-away process in an insect called the water strider. Conditional movement caused females to cluster around docile males and avoid aggressive males. Variation among groups caused by conditional movement allowed docile males to be maintained in the population, despite their selective disadvantage compared to aggressive males in every group containing both types.

The reason that cultural group selection is thought to be strong is because of various non-linearities. For example, a new cultural mutation need not remain at a low frequency within a group. It can quickly rise to a high frequency due to prestige bias or if it becomes established as a norm. However, non-linearities also exist for genetic group selection in the real world, even if they were absent from the initial models. Just as a single point mutation can be amplified by genetic and developmental interactions to have a large phenotypic effect on the individual, it can be amplified by social interactions to have a large phenotypic effect on the group. Nonlinearities have been demonstrated in virtually every laboratory experiment that involves the creation of groups (Goodnight and Stevens 1997). The phenotypic variation among groups is almost invariably much greater than expected on the basis of additive genetic effects. Once a social group is envisioned as a complex system, in which the phenotypic traits influencing fitness at any level reflect complex interactions among component traits under genetic control, then expectations about the balance between levels of selection must be extensively revised.

With my PhD student William Swensen, I took this to extremes by selecting at the level of multispecies ecosystems. In one set of experiments (Swensen et al. 2000a ), soil microbial ecosystems were selected for the ecosystem phenotypic trait of plant biomass. During the first ecosystem "generation", pots with sterilized soil and *Arabidopsis* seeds from a single seed bank (so that the plants didn't evolve) were colonized with 6 grams of unsterilized soil from a single well-mixed source. Initial variation in the ecosystems among pots caused by sampling error was negligible. Nevertheless, complex interactions within each pot amplified their differences in ways that influenced plant biomass. When the soil from the pots with the highest plant biomass (or lowest in a parallel experiment) was used to inoculate a new generation of pots, there was a response to selection, which is proof of ecosystem-level heritability (Goodnight 2000). In a separate set of experiments, we selected aquatic microbial ecosystems for the ecosystem-level traits of pH and the ability to degrade a toxic compound (Swenson et al. 2000b).

These results were published at about the same time that the term "microbiome" was coined, reflecting a dawning awareness that every multicellular organism is inhabited by an ecosystem of many thousands of microbial species numbering billions of individuals. The phenotype of a multicellular organism reflects a complex interaction between its genes and its ecosystem. In other words, evolutionary biologists must wrap their heads around the concept of gene-microbiome co-evolution in the same way that human evolutionary biologists must wrap their heads around the concept of gene-culture coevolution. Let there be no more talk about the rejection of group selection remaining valid for genetic evolution.

Yet another consideration involves the cost of providing public goods. Earlier I stated that there are no fitness differences in a win-win situation. By definition, a public good that can be produced at no cost to the provider is neutral as far as within-group selection is concerned. Any amount of variation among groups (including random variation) is sufficient for a no-cost public good to evolve by between-group selection, because it is not opposed by within-group selection. While the concept of a no-cost public good might be biologically unrealistic, there are many examples of public goods that can be provided at extremely low cost, including various forms of third-party rewards and punishments (Sober and Wilson 1998 ch 3). The conditions for the evolution of low-cost public goods are permissive because opposing within-group selection is weak, although not absent.

Collective decision-making is another example of a low-cost public good. It is well documented in the eusocial insects (e.g., Seeley 2010), where high relatedness within groups (=a large amount of genetic variation among groups) also allows the evolution of costly altruistic behaviors such as non-reproductive castes and suicidal predator defense. Once we realize that collective decision-making is a low-cost public good, we can predict that it will occur in a much wider range of groups such as fish schools, bird flocks, and ungulate groups, whose members are not and need not be closely related to each other (Couzin et al. 2011; Sontag et al. 2006).

This brings me to my final point about genetic group selection: Human evolution as a major transition. The concept of a major transition notes that the balance between levels of selection is not static but can itself evolve. When mechanisms evolve that suppress the potential for disruptive within-group selection, then between-group selection becomes the dominant evolutionary force and the group becomes so cooperative that it qualifies as a higher-level organism. The concept of a major transition is inherently about MLS. It was first proposed to explain the evolution of nucleated cells from symbiotic communities of bacterial cells in the 1970's, when the rejection of group selection was at its peak (Margulis 1970). Then it was generalized in the 1990's by John Maynard Smith (the former critic of group selection) and Eors Szathmary to include other major events in the history of life, including the first cells, multicellular organisms, eusocial insect colonies, and possibly even the origin of life as groups of cooperative molecular interactions (Maynard Smith and Szathmary 1995, 1999).

Maynard Smith and Szathmary were timid about describing human evolution as a major transition, confining themselves to the genetic basis of language. Everything we have learned since supports the view of human evolution as a series of major transitions, beginning at the scale of small groups and continuing at ever larger scales, as documented by Turchin (2015). The work of Christopher Boehm (1993, 1999, 2011 ) speaks most clearly to the concept of early human evolution as a major transition. Our closest relatives, chimps and bonobos, cooperate to a degree (bonobos more than chimps) but are also riven by disruptive competition within groups. Even cooperation often takes the form of small coalitions that compete against each other within the same troop. What made our ancestors different was the ability to collectively suppress bullying and other disruptive behaviors within the group, so that cooperating as a group became the dominant survival strategy. This, by definition, is a major evolutionary transition. Other accounts of early human evolution differ in their details, but they all can be seen as a shift in the balance between levels of selection, once the partitioning of selection within and among groups is made explicit. The most important point for the purposes of this essay is that the first human major transition, at the scale of small groups, was a genetic evolutionary event that made the capacity for culture and subsequent major cultural transitions possible. You can't tell the human evolutionary story without invoking genetic group selection.

## On Partial Equivalence

Standard science involves a contest among rival hypotheses that invoke different causal processes, such that one can be right and the other wrong. This contest takes place within MLS theory when we ask whether a given trait evolved by within-group selection, between-group selection, or a combination of both. There is a right and wrong to the answer that everyone can agree upon when the appropriate information has been gathered.

The discovery that the major theories of social behavior are not like this—that they are more like different accounting systems or languages for describing the same set of causal processes, was a major insight and decisive factor in the revival of MLS theory. However, this does not mean that the major theories of social evolution are equivalent in all respects. In what follows I will restrict myself to the comparison between MLS and kin selection theory.

One asymmetry is that MLS theory is a causal hypothesis, similar to Darwin's theory of natural selection, which can be stated in words and modeled mathematically in a variety of ways. Historically, it is literally an addendum that Darwin was forced to add to his theory when he realized that social adaptations can't evolve on the strength of relative fitness differences within groups. In contrast, kin selection theory is an attempt to represent social evolution in a particular mathematical form, $br-c>0$ (Hamilton's rule), where $c$ is the cost of altruism for the donor, $b$ is the benefit to the recipient, and $r$ is the coefficient of relationship. Hamilton's rule can be translated into MLS theory by reinterpreting $r$ as an index of variation among groups.

While Hamilton's rule is aesthetically pleasing and insightful for its simplicity, it owes its simplicity to a number of simplifying assumptions, such as additive genetic interactions and fitness effects. When we complicate the assumptions, Hamilton's rule loses its simplicity. For example, $r$ can become a compound term with many variables, including the frequency of the altruistic gene in the population, which therefore changes the value of $r$ every time gene frequency changes (Traulsen 2010). In the article by Birch and Okasha (2014) quoted at the beginning of this essay, no less than three versions of Hamilton's rule are provided and each is more complex than the intuitive version that most biology students are taught in college.

In some cases, the ability to express social evolution in the form of Hamilton's rule becomes impossible or so unwieldy that there are no benefits for doing so. As an example, consider the concept of equilibrium selection described earlier. Each equilibrium is locally stable but they differ in their adaptedness at the group level. Between group selection therefore takes the form of selection among locally stable equilibria rather than selecting for altruistic traits that are internally unstable within each group. This is easy enough to understand and model in terms of MLS theory, but very difficult, if not impossible, to render in the form of Hamilton's rule. Little wonder that MLS has become the theoretical framework of choice for the study of human cultural evolution, where complexities such as multiple local equilibria are the rule.

## Conclusion

I hope this essay has shown that a new plateau for the acceptance of MLS theory is both warranted and within reach. The basic tenets of MLS are easy to understand in plain language. The Averaging Fallacy is easy to spot and avoid once one becomes aware of it. There is an ample literature on genetic group selection. And MLS is an indispensable theoretical framework for understanding human evolution. All of this deserves to become the consensus view for scientists and the general public alike.

## Literature Cited

Aktipis, C. A. (2004). When to walk away: Contingent movement and the evolution of cooperation. *Journal of Theoretical Biology*, *231*(2), 249–260.

Birch, J., & Okasha, S. (2014). Kin Selection and Its Critics. *BioScience*, *65*(1), 22–32. http://doi.org/10.1093/biosci/biu196

Boehm, C. (1993). Egalitarian society and reverse dominance hierarchy. *Current Anthropology*, *34*, 227–254.

Boehm, C. (1999). *Hierarchy in the Forest: Egalitarianism and the Evolution of Human Altruism*. Cambridge, Mass: Harvard University Press.

Boehm, C. (2011). *Moral Origins: The Evolution of Virtue, Altruism, and Shame*. New York: Basic Books.

Bowles, S. (2009). Did warfare among ancestral hunter-gatherers affect the evolution of human social behavior? *Science*, *324*, 1293–1298.

Couzin, I. D., Ioannou, C. C., Demirel, G., Gross, T., Torney, C., Hartnett, A., … Leonard, N. E. (2011). Democratic Consensus in Animal Groups. *Science*, *334*, 1578–1580.

Eldakar, O. T., Dlugos, M. J., Pepper, J. W., & Wilson, D. S. (2009a). Population structure mediates sexual conflict in water striders. *Science (New York, N.Y.)*, *326*(5954), 816.

Eldakar, O. T., Dlugos, M. J., Wilcox, R. S., & Wilson, D. S. (2009b Aggressive mating as a tragedy of the commons in the water strider Aquarius remigis. *Behavioral Ecology and Sociobiology*, *64*(1), 25–33.

Fehr, E., & Gachter, S. (2002). Altruistic punishment in humans. *Nature*, *415*, 137–140.

Goodnight, C. J., & Stevens, L. (1997). Experimental studies of group selection: What do they tell us about group selection in nature? *American Naturalist*, *150*, S59–S79.

Goodnight, C. J. (2000). Heritability at the ecosystem level. *Proceedings of the National Academy of Sciences USA*, *97*, 9365–9366.

Hamilton, W. D. (1975). Innate social aptitudes in man, an approach from evolutionary genetics. In R. Fox (Ed.), *Biosocial anthropology* (pp. 133–155). London: Malaby Press.

Harman, O. (2010). *The Price of Altruism: George Price and the Search for the Origins of Kindness*. New York: Norton.

Henrich, J. (2015). *The Secret of Our Success: How culture is driving human evolution, domesticating our species, and making us smarter*. Princeton: Princeton University Press.

Henrich, J., Boyd, R., & Richerson, P. J. (2012). The puzzle of monogamous marriage. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *367*(1589), 657–69. http://doi.org/10.1098/rstb.2011.0290

Margulis, L. (1970). *Origin of Eukaryotic cells*. New Haven: Yale University Press.

Maynard Smith, J. (1964). Group selection and kin selection. *Nature*, 1145–1146.

Maynard Smith, J., & Szathmary, E. (1995). *The major transitions in evolution*. New York: W.H. Freeman.

Maynard Smith, J., & Szathmary, E. (1999). *The origins of life: from the birth of life to the origin of language*. Oxford: Oxford University Press.

Okasha, S. (2006). *Evolution and the levels of selection*. Oxford, UK: Oxford University Press.

Richerson, P. J., & Boyd, R. (2005). *Not by genes alone: how culture transformed human evolution*. Chicago: University of Chicago Press.

Samuelson, L. (1997). *Evolutionary games and equilibrium selection*. Cambridge, MA: MIT Press.

Seeley, T. D. (2010). *Honeybee Democracy*. Princeton: Princeton University Press.

Sober, E., & Wilson, D. S. (1998). *Unto Others: The Evolution and Psychology of Unselfish Behavior*. Cambridge, MA: Harvard University Press.

Sontag, C., Wilson, D. S., & Wilcox, R. S. (2006). Social foraging in Bufo americanus tadpoles. *Animal Behaviour*, *72*(6), 1451–1456. http://doi.org/10.1016/j.anbehav.2006.05.006

Swenson, W., Wilson, D. S., & Elias, R. (2000a). Artificial Ecosystem Selection. *Proceedings of the National Academy of Sciences*, *97*, 9110–9114.

Swenson, W., Arendt, J., & Wilson, D. S. (2000). Artificial selection of microbial ecosystems for 3-chloroaniline biodegradation. *Environmental Microbiology*, *2*, 564–571.

Traulsen, A. (2010). Mathematics of kin- and group-selection: formally equivalent? *Evolution; International Journal of Organic Evolution*, *64*(2), 316–23. http://doi.org/10.1111/j.1558-5646.2009.00899.x

Turchin, P. (2015). *Ultrasociety: How 10,000 years of war made humans the greatest cooperators on earth*. Storrs, CT: Baresta Books.

Williams, G. C. (1966). *Adaptation and Natural Selection: a critique of some current evolutionary thought*. Princeton: Princeton University Press.

Wilson, D. S. (1987). Altruism in mendellian populations derived from kin groups: the haystack model revisited. *Evolution*, *41*, 1059–1070.

Wilson, D. S. (2015a). *Does Altruism Exist? Culture, Genes, and the Welfare of Others*. New Haven, CT: Yale University Press.

Wilson, D. S. (2015b). Challenge to kin selectionists: Explain This! *This View of Life*.

Wilson, D. S., & Sober, E. (1994). Reintroducing group selection to the human behavioral sciences. *Behavioral and Brain Sciences*, *17*, 585–654.

Wilson, D. S., & Wilson, E. O. (2007). Rethinking the theoretical foundation of sociobiology. *Quarterly Review of Biology*, *82*, 327–348.