Review of Evolutionary Restraints: The Contentious History of Group Selection

Mark E. Borrello

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Herbert Gintis

George Santayana once famously said "Those who cannot remember the past are condemned to repeat it." Perhaps even those who remember the past may be condemned to repeat it, unless they learn sufficiently from it. Borrello adds a bit to the well-known history of the debate over levels of selection, but he does not help us understand what the real issues are, and how they might be resolved. Perhaps it is not his fault: the whole issue seems to be a hopeless muddle even in the hands of the most adept contemporary thinkers.

Biologists have debated the nature and status of group selection since the early twentieth century. The debate continues. Curiously, there have always been both extremely eminent supporters and equally eminent detractors of group selection, such as J. B. S. Haldane vs. Ernst Mayr (early years), John Maynard Smith vs. Stephen Jay Gould (recent past), and most recently Edward O. Wilson vs. Richard Dawkins. So pitched has this debate been that in reviewing Wilson's book The Social Conquest of Earth (which eloquently defends and extends group selection arguments), Richard Dawkins (who treats such arguments with characteristic distain) wrote "To borrow from Dorothy Parker, this is not a book to be tossed lightly aside. It should be thrown with great force." My more temperate and supportive review of Wilson's book, by the way, is published in BioScience and entitled The Clash of the Titans The paper is available from my web site.

To add fuel to the fire, in a response to a paper in Nature in 2010 by Wilson and coauthors Martin Nowak and Corina Tarnita that trashes inclusive fitness and extols group selection, some 150 well-known biologists wrote a vitriolic reply in a letter to Nature in 2010, resoundingly rejecting Wilson and coauthors' arguments. More heat, in my estimation, but less light.

I am an outsider to this debate. My training and most of my research until a couple of decades ago was in mathematics and economics. But I have come to work in biology as an adult, a situation that may have allowed me to avoid the emotional baggage attached to the dispute.

The group selection dispute shows the immaturity of contemporary population biology. No mature scientific dispute can sustain itself at so a high level of emotion and so low a level of progress for over a century without resolution. Indeed, most participants to the dispute agree that one can describe sociobiological behavior equally validly at the level of the gene, at the level of the individual (in a sexually reproducing species with a sequestered germ plasm), or at the group level (in species that live in groups engaged in social interaction). This admission, surprisingly, does not stop the disputants from intemperate diatribes at each other's expense.

Borrello's book does a competent if breezy and non-technical overview of this controversy, with some historical emphasis on particular papers presented by the disputants at different times. He does, however, seriously underestimate the importance of R. A. Fisher in laying the groundwork for the position of the Oxford school in this research area, and he has a long, unoriginal, and irrelevant analysis of Lamarckism. However, Borrello makes no attempt to cut through the verbiage and miscommunication to put the issue into insightful theoretical perspective. History, for Borrello, is not one damn thing after another---it is the same damn thing over and over!

So let me here explain what is really going on in the controversy over group selection. Population biology is based on careful accounting at the level of the gene (this is why Ernst Mayr criticized J. B. S. Haldane's work as "beanbag genetics"). Indeed, all of Darwinian evolution can be analyzed, at least in principle, in terms of changes in gene frequencies and correlations among genes in the genome. The two sides to the debate over group selection differ as to how correlations among genetic loci in the genome are to be treated. In the tradition of Fisher and Haldane, inspired by the mathematics of heredity developed to deal with animal husbandry, only the additive component of a gene's contribution to the fitness of its carriers need be analyzed because "evolution only sees the additive component." Those in the tradition of Ernst Mayr and Theodosius Dobzhansky, by contrast, consider the genome itself as a unit that is subject to natural selection, and it is the cooperative interaction of genes in the genome that governs its evolutionary success.

This distinction is then carried over from interactions among genes in the genome to interactions among individuals in a social species: inclusive fitness theorists, the heirs to the Fisher-Haldane gene's-eye view, reduce complex interactions among individuals in a social species to simple influences at single genetic locus (inclusive fitness), whereas the heirs to the Mayr-Dobzhansky tradition take social cooperation to involve complex dynamical and nonlinear interactions (multi-level selection). The inclusive fitness adherents argue that the genome cannot be an object of selection because it is broken up in every generation through meiosis and crossover, while the gene is conserved intact over many generations. The multilevel selection adherents claim that inclusive fitness analysis ignores all the substantive complexities of social interaction that in fact account for the evolutionary success of a social species.

My own studies have provided me with a third perspective. First, inclusive fitness analysis is extremely important and valid under almost all circumstances in dealing with sexually reproducing populations. Its strength comes from the fact that its reasoning is on the level of a single genetic locus. Popular expositions obfuscate this point by implicitly, without argument, treating a complex social behavior as governed by a single genetic locus---the so-called "phenotypic gambit." The correct analysis, that proposed by William Hamilton in 1964, shows that genes are utterly selfish in the sense popularized in Dawkins' great book "The Selfish Gene." What this means is that the conditions for the evolutionary success of a gene are distinct from the conditions under which it promotes the fitness of the reproduction population. Thus individual genes have absolutely no regard for the evolutionary success of the species in which they reside.

For instance, take the basic inclusive fitness equation, Hamilton's Rule. This says that if an allele at a genetic locus causes a behavior in the individual (the donor) that costs the individual a fitness loss c, and provides a fitness benefit b to another individual (the recipient), then the allele will increase in frequency provided b r > c, where r is the degree of relatedness between the donor and the recipient. The total contribution of the allele to the population is then b-c, which must be strictly positive provided that the degree of relatedness is a probability (the usual case), and b,c > 0. This is because b - c = b(1-r) + br - c > b(1-r), which is non-negative. However, there is no reason to limit the analysis to b, c, and r having particular signs. Hamilton's rule holds no matter what the sign of the cost c (which becomes a benefit when less than zero) and the benefit b (which become a cost when b is less than zero). Thus Hamilton's rule says that a selfish gene that helps its carrier by hurting other members of the population is just as capable of evolving as an altruistic gene that induces its carrier to take a fitness hit in order to confer a fitness benefit on others, despite that the former reduces mean population fitness while the latter increases mean population fitness.

For instance, suppose b and c are both negative, which occurs when the allele helps its carriers by hurting other members of the population. In that case b - c, the fitness contribution to the population, will be negative unless individuals interact almost exclusively with their genetic relatives. For instance, suppose b = -0.4, c = -0.3, and r = 1/2. Then b-c = -0.1, which is negative, but b r - c = 0.1, which is positive, so Hamilton's rule is satisfied.

The validity of inclusive fitness theory allows us to formulate the central problem of sociobiology as follows: Individual genes are utterly selfish, yet evolutionarily successful species consist of genes that predominantly cooperate with one another (this is the reason there is an "appearance of design" in multicellular organisms), and evolutionary successful social species consist predominantly in individuals who cooperate in a manner furthering their joint biological interests. By the very fact that inclusive fitness theory abstracts from interactions among loci, this theory cannot help solve the central problem of sociobiology.

The irony in the debate over group selection is that the theorists involved in the debate fight endlessly over it even though they know that there is nothing to fight about, while the onlookers, such as those tempted to read this book, believe the debate must be over something real and of momentous importance. Usually, onlookers think the debate is about whether "biological altruism" can exist, and more specifically, whether human society is based on self-interest or truly moral behavior. That is a very important question, to which Samuel Bowles and I devoted a whole book: A Cooperative Species (Princeton University Press, 2011). We conclude that our success as a species is based on the essential morality embedded in human nature. But this has nothing to do with the group selection debate as it is properly formulated. We argue in this book that the fact that humans evolved in small groups (hunter-gatherer societies) is central to the evolution of human morality, but our analytical models are equally well described in terms of inclusive fitness (applying the phenotypic gambit) and multi-level selection. Indeed, the models themselves use neither concept, but are simply sets of equations that represent plausible dynamics underlying the current constitution of the human genetic structure.