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Nicholas S. Thompson

Clark University, nthompson@clarku.edu

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Vehicles all the way down?

Nicholas S. Thompson

Departments of Biology and Psychology, Clark University, Worcester, MA
01610. nthompson@vax.clarku.edu

Abstract: One approach suggested by a reading of the target article is that we jettison entirely the notion of replicator and focus on the formation and dissolution of vehicles down through the generations.

Wilson & Sober's (W & S's) target article is important because it reveals some onerous and unnecessary assumptions that have afflicted the debate about group selection from the start. The authors successfully debunk the notion that there is anything privileged about the individual level of analysis. In so doing, they make explanation at the group level respectable by demonstrating that any form of argument sufficient to explain adaptation in terms of consequences to individuals will sometimes be strong enough to explain adaptation in terms of consequences to groups. This is an important accomplishment.

Perhaps even more important is the doubt that the target article casts on the assumption that replicators exist distinct from vehicles. Genes are replicators but they are so by definition, not by observation. So if there is no such distinct thing as a replicator, then it follows that there is no such thing as a gene. Surprising though it may seem, this is a difficulty anticipated by Dawkins (1976, p. 35) when he writes, "To be strict, this book should be called not *The Selfish Cistron* nor *The Selfish Chromosome*, but *The Slightly Selfish Big Bit of Chromosome and the Even More Selfish Little Bit of Chromosome*." If this passage can be fairly read in terms of his later work (Dawkins 1982a), Dawkins seems to concede here that replicators are ephemeral. And to rescue them in this passage, he seems to bring to bear the concept of "common fate," which, of course, means that he is defining replicators as W & S define a vehicle.

Should we jettison the notion of replicator entirely and focus exclusively on the concept of common fate? The hierarchy of organization would then be conceived as a succession of levels of organization each with a characteristic degree of coherence in its elements. And vehicles would be conceived as forming and dissolving down through the generations. The notion of natural selection could be retained because, strictly speaking, it does not require genes or even direct descendants; all it requires is that the presence of a configuration of elements in one generation makes more likely the presence of the same configuration in the next generation. Then, from considerations raised by Wilson & Sober, we would expect "organisms" to arise at discontinuities in the degree of coherence between levels of the hierarchy. Wherever we find a level with a high degree of coherence nested within a level with a low degree of coherence, there we should expect to see the evolution of "organisms."

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The maintenance of behavioral diversity in human societies

Christopher Wills

Department of Biology 0116, University of California, San Diego, La Jolla, CA 92093. cwills@ucsd.edu

Abstract: Models of group selection are complex, awkward, and tend to be balanced on a knife edge of perilous assumptions. Sociologists and geneticists apply them to something as complex as human society at

their peril. I suggest an alternative model based on the maintenance of genetic heterogeneity for behavior within groups. This can occur by means of slight behavioral alterations in the group as a whole that take place whenever one type of behavior tends to predominate.

This target article by Wilson & Sober (W & S) gives a detailed and thoughtful historical survey of the vicissitudes of group selection as it has been applied to biological systems in general and to human behavior systems in particular. W & S make the plea that group selection, despite its chequered history, can be applied profitably by biologists and sociologists to such complex systems, to help explain the maintenance of traits such as altruism that are deleterious to individuals but beneficial to the group. They also point out that the idea of group selection is making a comeback among evolutionary biologists. Their primary human example is the Hutterites, whose unusual social structure revolves around the Christian ideals of selflessness, love of one's neighbor, and cooperation to help maintain the integrity of the group. These traits are, Lord knows, not prominent in the behavior of many human groups other than the Hutterites. They are, however, present occasionally, a point to which I will return.

To begin with, there are arguments about group selection that W & S do not dwell on. One point, as I have discussed elsewhere (Wills 1989), is that if groups persist for long periods of time before becoming extinct, then group selection will be excruciatingly slow. A second is that the balance between the individual disadvantage and group advantage of some genotype must be a very delicate one – too great an individual disadvantage and the gene is rapidly lost before it has a chance to persist long enough to permit the group to survive. These are among the reasons why many evolutionists feel very uncomfortable about group selection; to make it work, assumptions often have to be piled one on another, like Pelion upon Ossa.

W & S list a large number of papers that they claim present group-selection models, as part of a rising tide of group selection *redivivus*. One of mine (Wills 1991), dealing with the maintenance of genetic polymorphism at the MHC (major histocompatibility complex) region, is among them. The argument I made in that paper, one that I am expanding elsewhere with a colleague (Wills & Green, in press), is not really a group-selection argument. Let me explain what I meant, and use it as a jumping-off place for a critique of group-selection models that assume mixtures of behavioral types that are rigidly controlled by alleles of genes influencing behavior. These are models of the kind dealt with by W & S.

My model suggested that genetic polymorphism at MHC, a set of loci that is at least partially concerned with disease resistance and susceptibility, might be maintained in the following fashion. If an allele conferring susceptibility to a disease becomes common in the population, then the disease organisms can multiply and the allele will be driven down in frequency. Below a certain frequency, the disease organisms have great difficulty spreading and are forced to retreat to refugia, from which they can always reemerge. Meanwhile, other alleles rise in frequency, allowing other diseases to emerge from their refugia and drive them down again. Given enough diseases and enough alleles that are affected differentially by the different diseases, a stable polymorphism results as the various alleles pop up and are pushed down.

This is not group selection, for two reasons. First, the system works well with just one host population (though it requires a number of parasite populations). Second, there is an immediate advantage to an individual living in such a polymorphic host population. Even though that individual may be susceptible to one or more diseases, it finds itself in a population with other individuals that are resistant to those diseases. Those other individuals keep the numbers of the disease organisms in check, so that the first individual is less likely to succumb to the diseases to which it is susceptible. Some hosts do die each