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# Group Selection Is Dead! Long Live Group Selection?

AYELET SHAVIT AND ROBERTA L. MILLSTEIN

**We live in interesting times. Two** well-known biologists—E. O. Wilson and Richard Dawkins—and some of their well-known colleagues, who used to employ broadly similar selection models, now deeply disagree over the role of group selection in the evolution of eusociality (or so we will argue). Yet they describe their models as interchangeable. As philosophers of biology, we wonder whether there is substantial (i.e., empirical) disagreement here at all, and, if there is, what is this disagreement about?

We argue that a substantial disagreement over the processes that caused eusociality best explains this debate, yet the common practice of using overarching definitions for "group selection" and "kin selection" renders empirical differences difficult to detect. We suggest Michael J. Wade's use of these terms as a basis for models that reveal different selection processes. Wade's models predict different outcomes for different processes and thus can be tested.

Some background: Thirty-three years after the publication of *Sociobiology: The New Synthesis* (Harvard University Press, 1975), E. O. Wilson seems to be making an almost 180-degree turn (Wilson 2008). Back then, Wilson accepted a broad definition of "kin selection" as the favor or disfavor of individuals based on kin relatedness, but now he claims this concept applies only to collateral relatives (i.e., those other than parents and offspring). Back then, Wilson thought eusociality was all about relatedness, whereas now he argues for a minor—if any—explanatory role for kin selection. Although Wilson has always claimed to support group selection theory, only recently has this inclination channeled into a specific mathematical model of group selection and against the centrality of kin selection. One thing has not changed: Wilson's very rich and well-organized assembly of recent empirical findings.

His opponents, who favor kin selection over group selection, target his interpretation rather than his facts. Indeed, both sides declare that their models are translatable, that is, they could agree with any set of data the other model agreed with (Dawkins 1982, Wilson and Wilson 2007). If this disagreement were purely about terminology, one would expect the community to gradually lose interest in it. This has not happened. Another option is that this debate continues because it is semantic in a nontrivial way: that is, the models agree with all the data but differ greatly in their heuristic value. In that case, one would expect many methodological comparisons of model performance—for example, comparisons of models' precision, generality, accuracy, complexity, or elegance—for various species and social phenomena in the lab and in nature. Yet these are not a central part of the debate either. Rather, it seems there is no given phenomenon both sides use; instead, disputants clash on how to define or describe the phenomenon that our models attempt to fit to. In short, they disagree over what it is that we see when some ants walk by.

For Wilson and Wilson (2007), a group is any aggregation of individuals that is small compared with the total population and consists of individuals interacting in a nonrandom way that affects each other's fitness. This is an extremely abstract understanding of what constitutes a group, one that fits many kinds of cases and is almost completely unconstrained by any particular population structure, dynamic, duration, or size. Nor does it require groups to multiply as anything like cohesive wholes in order to acquire heritable variance in fitness. Such a broad definition of "group" is central for Wilson and Wilson's definition of group selection: "the evolution of traits based on the differential survival and reproduction of groups." Such a group selection model does not differ empirically from the similarly broad definition of kin selection: "selection affected by relatedness among individuals" (Foster at al. 2006). Again, no particular population structure constrains the application of this kin selection model. The difference lies in model structure: whereas the group selection model partitions the overall selection in the population into "within-group selection" and "between-groups selection," alternative models—kin selection, reciprocity, indirect reciprocity, or mutualism—consider such partitioning unnecessary, since they all claim that what enhances group fitness always enhances the inclusive fitness of each member in the group (or rather, what Dawkins "only partly facetiously" describes as "that property of an individual organism which will appear to be maximized when what is really maximized is gene survival" [Dawkins 1982, p. 187]).

This theoretical difference in model structure does not necessarily emphasize different causal factors, because the contexts that can affect the frequency of altruists—population structure and ecology—can be captured by both models (Foster et al. 2006, Wilson 2008). The contexts therefore do not constrain

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either model, as both measure the evolutionary outcome only in gene frequencies, not as the process of evolving a new level of organization (Griesemer 2000). So, argue Foster and colleagues (2006), if E. O. Wilson's new group model does not generate facts unattainable otherwise, why accept his definition of kin selection rather than Maynard Smith's original definition—the evolution of characteristics that favor the survival of close relatives of the affected individual? And when Wilson states that "the final step to eusociality can occur with the substitution of only one allele or a small set of alleles" (Wilson 2008), why not call this allele for staying in the nest—which is easily recognizable by an arbitrary marker identifiable in other ants (such as an odor) and promotes favor of those ants—by Dawkins's original term, "green beard effect"? Yet Wilson asks in return, why not go back to Darwin's original explanation of group selection? Thus the debate again seems to be over terminology, this time with a historical twist.

But why should biologists care, as they obviously do? If the disagreement were mainly about choosing among interchangeable perspectives for the same phenomenon, a choice based on personal taste, historical uses, or heuristic values of group or kin models, one would expect the debate to gradually dissolve in the first two cases and become pragmatic and methodology based in the third. Since the debate has neither dissolved nor turned pragmatic, and since we assume the debate is a rational one, we suggest the remaining explanation as the best one: Wilson and Dawkins disagree over semantics because both hope for their different concepts and models to refer to different evolutionary processes in the world, with each maintaining that his preferred evolutionary process is the more prevalent. To use Dawkins's terms, even when modestly arguing over the flipping picture we see in a Necker cube, the nonmodest aim remains to decipher the picture we see from an East African mountain: are the small spots below insects or buffalos (Dawkins 1982)?

When Wilson looks at a social group he sees a unit that is a target of a selection, while Dawkins sees an illusory byproduct of a different selection process acting at a single level of organization: gene selection. They disagree the way they do *because* they aim to accurately represent empirical facts, but since both sides employ overly broad definitions for group, group selection, and kin selection, it becomes very difficult to identify a specific fact—for example, a particular population dynamic or structure—to distinguish between these models in a particular case. We think this situation is unfortunate. Whether or not certain subpopulations have heritable variance in fitness is an empirical question, whatever you choose to call these entities (Griesemer 2000). Luckily, an alternative is already present in the literature. Wade (1978, 1985) defined group selection and kin selection in accord with different population structures, so his constrained models could clearly refer to distinct selection processes that he and his colleagues then compared in the lab or in the field. Dawkins and Wilson may object that Wade's definitions are too narrow. They would be right in the sense that his definitions do not cover many kinds of cases, yet that does not imply that his definitions do not cover many cases. They do. Indeed, narrow definitions—those that restrict the kinds of cases—give us tools to determine what is and what is not happening in a given population, whereas the broad definitions used by Dawkins and Wilson will forever talk past each other without resolution.

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