

Why the levels of selection problem seems so difficult to resolve

1. Populations seem to do things that represent effects of group selection (for example, ecologists for a long time thought populations had built-in regulating devices)
2. Populations have traits that, at least at first, appear not amenable to analysis below the population level, or seem to be traits of populations not individuals (for example, sex ratios)
3. Most animals seem to live in social groups, and many of the most familiar ones seem to cooperate in ways that might be construed (at least, at first) as suggesting group level selection.
4. Selection, as better versus worse in the current environment, is, overall, very difficult to incorporate into the mathematical formulations of population genetics. It is easier to incorporate selection as a group-level force than as an individual-level force (e.g., "average fitness" (of individuals) within a population is often translated to mean "average fitness of the population," and this leads to comparing population fitnesses and thus to an assumption of group selection. The lure of this kind of formulation has led to some royal goofs, such as "Haldane's Dilemma," the conclusion that populations' genetic "loads" of mutations somehow make it sometimes too expensive for a population to evolve [I gave an account of this problem in in my 1988 paper cited -- and used in part, but I didn't use the relevant part(!) -- in Handout 14; genetic load is also discussed in Handout 24].
5. The reasons for effectiveness of selection (amount of difference, heritability of differences, generation time or cycling time) are not easy to apply at different levels in the hierarchy of organization of life so as to reach the cleanest, most satisfying conclusions (for example, see my effort on p. 38, fig. 3, in *Darwinism and Human Affairs* where I couldn't come up with nice unequivocal differences between sets of open and black circles. Some of you ran into this problem considering "cycle time" in sperm when thinking about rates of evolutionary change via selection in sperm and eggs (the reason cycle or generation time is listed is that it results in "flushes" of variation through large numbers of descendants; it's the large number of sperm involved in a single fertilization event that produces much heritable variation, largely through recombination).
6. Humans are exhorted to think in terms of benefits to others and to the entire group to which they belong, so that it is difficult (or expensive) for individual humans to think (or admit) that humans might have evolved to promote individual reproductive success. Culture is constructed as a group-level phenomenon (I suggest, because humans have forever competed as groups), and this is confusing even if culture ultimately turns out to be systems of collective decision about the limits of confluences of interests among groups and subgroups that result in sets of moral, legal, and social rules about how far individuals and subgroups can go in serving their own interests
7. Humans do particular things, or live kinds of lives, that seem impossible to explain in terms of individual-level selection -- that therefore seem to be falsifiers of the notion of individual-level selection being universal or always outdoing group-level selection.
8. Genetic drift and group selection are both seen as not pernicious ideas, relative to human conduct and how humans view one another, while individual-level selection sometimes is seen as arguing for a justification of selfishness. Thus, drift doesn't imply that some traits are "better" than others, as differential reproduction does (to some people sometimes); and group selection implies benevolent behavior to all members of the group (but watch out if you're not "in" some particular group!).
9. Cooperation, which causes us to think in group terms, and of group-level selection, is actually difficult for humans to understand as a method of competing. Instead, it is often thought of simply as an alternative to competition. Whether we can turn our historical inclinations to turn everything into a "we-they" proposition (even left-and right-handedness!) into cooperative interdependence of a non-destructive sort, world-wide, seems to be the biggest problem facing humanity.
10. Some of these sometimes quite different reasons for difficulty may combine to make people working in evolution, ecology, behavior, and population genetics continue to work for and produce results that they describe as evidence of group-level selection, and that are not quickly and decisively understood by readers. So the whole problem seems to get perpetuated as a fuzzy, hazy kind of failure of resolution.

So how do we solve the problem? Just by continually chipping away at it. Look at one behavior after another and try to develop hypotheses that call for stark differences between the results of group-level selection and individual-level selection; and see what keeps falling out.