# THE RETURN OF THE GROUP*

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**1. A Slice of History.** Once upon a time in evolutionary theory, everything happened for the best. Predators killed only the old or the sick. Pecking orders and other dominance hierarchies minimized wasteful conflict within the group. Male displays ensured that only the best and the fittest had mates. In the culmination of this tradition, Wynne-Edwards (1962, 1986) argued that many species have mechanisms that ensure groups do not over-exploit their resource base. The "central function" of territoriality in birds and other higher animals is "of limiting the numbers of occupants per unit area of habitat" (1986, 6). Species with dominance hierarchies, species with lekking breeding systems, and species with communal breeding regulate their populations. These social mechanisms have population regulation as their "underlying primary function" (1986, 9). Wynne-Edwards argued that these mechanisms evolve through group selection. Populations without such mechanisms are apt to go extinct by eroding their own resource base.

Group selectionist ideas were motivated by the perception of altruistic behavior in the natural world. It is hard to see how altruism could evolve by individual selection, for in mixed populations the selfish do better by free-riding on the others. But it is not hard to see how groups of altruists would out-compete selfish groups. Sadly for these visions of benevolence, group selection fell on very hard times. Lack (1966) argued that reproductive restraint *can* benefit the individual. More generally, Maynard Smith (1964) and Williams (1966) argued that once made explicit, the assumptions on which group selection relies seem very implausible. In sum, the reactions to group selection took three forms: the first was an alternative conception of evolution and the units of selection, the second was an alternative explanation of altruism and other explanatory targets

of group selection, and the third was a direct critique of group selectionist explanations.

Williams, and following him Dawkins, argued that the real agents in the selection game are genes. In reproduction, some of the germline genes of an organism are copied and passed on to their offspring. Genes are replicators. They root lineages of copies of themselves. Some lineages are long and bushy, others are short or thin. For the most part, these differences are no accident: genes exert phenotypic power on the world in ways that affect their copying propensity. The adaptive features of organisms ultimately benefit the genes responsible for them, for the consequence of adaptive improvement is the proliferation of genes that rebuild those adaptations in descendant generations. The fundamental cause of selection is the differential capacities of replicators; its fundamental consequence is the differential growth of replicator lineages. On this conception, organisms are not copied. Reproduction is not the replication of organisms. Organisms are not the beneficiaries of adaptations for they cannot make more of themselves. Rather, organisms are vehicles or interactors.[1] Vehicles interact with their environment as a cohesive whole. They are structured units, units with effects on one another, effects with downstream consequences on replication propensities. Their differential success *vis-à-vis* their ecological competitors causes the differential success of replicator lineages *vis-à-vis* their genealogical competitors.

The second blow to group selection was the articulation of explanations of the most striking examples of altruistic animal behavior that seemed to leave no room for group selection. The most striking examples of cooperation—the complex divisions of labor amongst the eusocial insects—have come to be seen as the result not of selection at the level of hives or communities, but rather as the result of kin selection. Hamilton showed that in calculating an organism's fitness we should consider not just that organism's offspring, but also the contribution that organism makes to the direct fitness of its relatives, discounted by their genetic distance. Indirect fitness benefits are central to the evolution of the spectacularly altruistic behaviors of social insects.

The critics of group selection also point to a deep problem for Wynne-Edward's picture of restrained groups out-competing profligate ones. Al-

[1] "Vehicle" is Dawkins' term, "interactor" is Hull's (Dawkins 1982; Hull 1981, 1988). They are often taken to be equivalent, but that is a mistake. Hull's notion of an interactor is an attempt to capture a general functional role in evolution, to capture the way in which competition impacts on differential replication. Dawkins' idea of the vehicle is an attempt to characterize the distinctive evolutionary role of organisms. The central message of his most important work is that genes act adaptively on aspects of their environment outside the body of the organisms in which they reside. Replicators do not always act by constructing vehicles. In this paper, neither term is wholly apt. For I think there is an ambiguity within the group selection debate between the general notion of interaction and the more restrictive organism-like idea of the vehicle. But as Wilson and Sober use "vehicle," I shall too.

truistic groups seem very vulnerable to subversion from within. Imagine rabbit populations differing in levels of reproductive restraint. Restrained groups, let us suppose, delay first breeding. Restrained groups do much better in harsh winters, for most rabbits in profligate groups starve. Even so, if there is migration between groups, or if more fecund rabbits arise easily in the population, they will gain the benefits of living in a restrained group without paying the costs. Hence, the fecund will white-ant restraint. Moreover, the faster generation time of individual selection and the greater variety of individuals, suggests that in a race between the two selection processes, individual level selection should win. No one claimed that group selection was inherently impossible. Rather the claim was that very special conditions are needed before it works.

So group selectionist ideas fell on very hard times in mainstream evolutionary theory. But they are now making a comeback, due mostly to the work of D. S. Wilson.[2] It is that comeback I consider in this paper. The central ideas involve: (a) the idea that group selection is a hypothesis about vehicles, not replicators; (b) reinterpreting kin selection and reciprocal altruism as instances of group selection; (c) unveiling the excessively strong assumptions implicit in those analyses that suggest group selection must be weak or rare; (d) some suggestive examples of group selection in operation. Let me unpack these cryptic remarks.

**2. The Return of the Group: Trait Group Selection.** The best way to interpret group selectionists is to see them as claiming that groups function in evolution in the same way organisms do. That is, group selectionist hypotheses are about vehicles, not replicators. So a group selectionist can agree that the only replicators are genes; they think though that some vehicles are groups. So group selection is independent of the gene's eye conception of evolution. The idea that group selection is a hypothesis about vehicles opens the door for a revival of group selection, but is by itself insufficient. Even once we have made the replicator/vehicle distinction, group selection can seem unlikely if we have an overly fancy conception of vehicles. Wilson and his allies think our standard example—the vertebrate organism—can give us a misleading picture of vehicles. For such organisms are extraordinarily complex, co-adapted, and enduring. As Dawkins has emphasized, they have a very distinctive developmental sequence. They have determinate boundaries and they act on their envi-

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[2]D. S. Wilson's take on these issues has been developing over some years. See especially his 1983, 1989 and 1990, 1993, forthcoming a and b. Sober has been a powerful ally, especially in their recent collaborations; see Wilson and Sober 1989, 1994, and forthcoming. The idea that kin selection is an instance of group selection has been independently developed by Colwell; see Colwell 1981. Hamilton accepts that Wilson's line on kin selection is at least one possible reading of his work; see Hamilton 1975.

ronment as cohesive wholes. If every vehicle must have these character-
istics, then not many collectives will count.

Wilson has argued that we should not restrict our idea of a vehicle to
collectives which are co-adapted and complex. His argument depends on
drawing a parallel with the evolution of individual organisms. Organisms
are collectives or assemblages of cells. In the paradigm cases, they are
assemblages in which competition between cells has been suppressed. But
Buss (1987) showed that not all cell-assemblages have a full suite of ad-
aptations that suppress that competition. Those adaptations arise through
a history of cell-assemblage competition. Organisms must have been ve-
hicles before they were fancy vehicles. Similarly, obvious group level ad-
aptations are products of a long history of group selection, not precon-
ditions of its beginning.[3]

Wilson and friends therefore propose to identify a vehicle through the
idea of common fate. An organism is a vehicle rather than a population
of cells because those cells share a common fate. Similarly, a group of
beavers in a dam is a vehicle if their fitness is linked together on a common
causal trajectory. Beaver traits that affect that trajectory for better or
worse can be visible to selection through the fate of that beaver collective.
Obviously, common fate comes in degrees. No one suggests that the fate
of the beavers is as interconnected as the fate of the cells of one beaver.
More importantly yet, common fate is defined on a trait-by-trait basis.
Beavers, unlike cells in a single beaver, vary in fitness. Still, if the beavers
cooperate in the construction and maintenance of their dam, then that
characteristic will have a common effect on the beavers in the dam. Those
beavers will be affected and in the same way by this feature of its members,
and hence with respect to this trait—the dam building trait—the beavers
share a common fate.

Thus Wilson introduced and defended the idea of "trait groups": pop-
ulations which have a common fate with respect to some trait. Trait groups
are groups of organisms each of which feels the influence of the others
with respect to some trait. So if the trait is that of making warning signs,
it is the group of beavers that are in earshot of each others' tail slaps. If
the trait is dam building, it is the group of beavers that live and shelter in

[3]Friends of Dawkins' idea of the extended phenotype are well-placed to resist this argu-
ment. He argues that we should not assume that the phenotypic effects of replicator teams
come packaged as discrete co-adapted vehicles. If we could see the evolutionary history of
the organism itself, there would be a stage at which important phenotypic powers of genes
were expressed *neither* as adaptations of a cell, *nor* of organisms. The evolutionary history
of traits central to the invention of the organism did not depend on the selection of diffuse
organisms, but instead depended on selection for adaptive effects which were not features
of vehicles. Similarly, there is a point in the evolutionary history of adapted groups in which
genes had effects which were not expressed as traits of any vehicle. So we can think that
termite colonies are vehicles, and we can doubt that their less co-adapted precursor groups
are, without thinking that adaptations of groups evolve by selection on individual organisms.

the dam. Different traits will pick out different groups. In the most obvious examples, these groups are homogenous with respect to the trait in question. So our trait groups would be beaver groups in which all the beavers can hear each others' signals; or the group of beavers all of whom live in the dam they maintain jointly:

> . . . every trait has a "sphere of influence" within which the homogeneity assumption is roughly satisfied. It is the area within which every individual feels the effects of every other individual. I have termed this population the trait group . . . to emphasise its dependence on the particular traits being manifested." (Wilson 1980, 22)

However, trait groups need not be homogeneous with respect to the trait whose evolution is of interest to us. Kin groups of mixed altruists and nonaltruists are a single group, as are mixed groups of cooperators and defectors in social interactions. So a trait-group playing a role in the evolution of T is not necessarily a group of organisms all of whom have T. It is a group of organisms all of whom are roughly equally affected by the same group of T-bearers. All the beavers that live in a dam are a trait group, even if a few free-ride. For all these beavers, and only these beavers, are in "the sphere of influence" of a these dam builders even if they are not all themselves dam builders.[4]

A group of beavers in a dam is a spatially distinct group. But trait groups need not be spatially distinct in this way. A beaver that warns only blacktailed beavers forms a trait group: the group of beavers in the "sphere of influence" of the bearers of that trait. It does so even if these beavers are not spatially segregated from the rest. The fact that trait groups need not be spatially segregated enables us to see kin groups as trait groups. If trait groups are vehicles, kin selection is not a superior alternative to group selection, but a version of it. For altruism towards kin generates trait groups, the organisms all of whom are potential beneficiaries of that aid. This division of the population into groups is essential to the evolution of altruism. Within the kin group, the defector does better than his altruistic sibs. For the defector enjoys the benefits of aid without bearing the cost of giving it. A female lioness that did not allow her sisters' cubs to suckle would improve the prospects of her own reaching maturity. But a pride of altruist lions will "fledge" more cubs than a mixed group, which will do better than a wholly defecting pride. So if the boost from altruism is

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[4]Wilson does not restrict trait groups to organisms within the one species; one of his examples is of mixed-species flocks of birds. So the exact definition of trait groups is an issue of some delicacy. Though beaver predators are within the sphere of influence of the dam building trait, they are not within the trait group, for a good dam impacts on their fitness in a direction opposite to its influence on the beavers. But why aren't beaver fleas in the trait group? They seem like lazy beavers in the dam: they benefit without aiding. So if the defecting beaver is in the trait group, perhaps so should be the beavers' fleas.

big enough, and the cost is small enough, the average fitness of the altruist can be greater than the average fitness of the defector. Hence when the kin groups dissolve back into the general population before the next round of breeding, the proportion of altruists can rise despite free-riding in mixed groups.

Kinship is important, for it plays the central role in generating variation between groups. Since kin resemble one another, kin groups with one altruist are likely to have more than one; similarly, with selfishness. So the traits in question are not distributed randomly across groups. Random distribution, of course, depresses variation.

The same reasoning suggests that the evolution of reciprocation, too, frequently involves vehicles composed of individual organisms. Wilson and Sober (1994) unveil a most striking thought experiment with this as its moral. They depict a cricket population that feeds on lilies scattered across a pond. The problem for the crickets is to get from one lily to the next. Wilson and Sober imagine the evolution of cooperative navigation across the pond, as pairs of crickets evolve the capacity to row between lily pads on dead leaves. In their view, the required coordination evolves by selection on pairs. Crickets better able to coordinate with their partners are fitter than their clumsier colleagues. But this adaptive advantage is visible to selection only through the increase in efficiency with which *a pair* reaches a lily pad. So the pair is a vehicle. With respect to each trip, the pair share a common fate, and hence coordination evolves by group selection. The pair is a vehicle, even if these are the only cooperative interactions between crickets; even if a cricket rarely has the same partner twice; even if the great bulk of the cricket life cycle is between trips.

Evolution continues, as evolution will. A selfish mutant arises which casts adrift its partner at the end of the trip. It does well when its partner is naive, but poorly when paired with another selfish morph, for each has a tendency to drown the other. Despite group selection in favor of cooperation (for cooperative pairs do better than selfish pairs) within-pair selection favors the mutant and causes the selfish behavior to spread. More evolution: eventually a suppresser morph arises that prevents the selfish morph's behavior by clasping it when the two arrive at their destination. The clasping morph spreads through the whole population by group selection alone, for whatever the nature of its partner, the two crickets benefit equally from every trip. There are no within-pair fitness differences. Throughout this whole evolutionary dynamic, Wilson and Sober think the pair is a vehicle. It is the beneficiary of the joint behavior whose benefit is distributed over its members.

This picture of water cricket evolution suggests that the "subversion problem" is much overstated. That problem depends on the idea that groups are fairly large, they persist for a number of generations, and they

are unlikely to have effective defenses against subversion.[5] If water cricket evolution is evolution by group selection, these assumptions are unwarranted.

Even those very skeptical about group selection have always agreed that there might be a few examples of group selection in action. So, for example, Wade and his students were able to show that group size in flour beetles responds to selection (Wade 1978). More important, though also more controversial, was the evidence for the role of group selection on sex ratios. Selection at the level of individual organisms tends to favor a 50/50 ratio. For if the sex ratio is disturbed from a 50/50 balance, a parent maximizes its grand-offspring, all else being equal, by producing the rare sex. However, it is easy to conceive of circumstances in which selection on groups would favor an unbalanced sex ratio. Imagine insects that feed on rich but widely scattered resources. The resource is typically found by one or a few mated females, whose progeny consume the resource. They mate and the females disperse. Almost all die, but a few find new bonanzas. The more that disperse, the more likely it is that there will be some successful searchers. A female-biased sex ratio allows more colonizations. Under circumstances like these a female-biased sex ratio can evolve, and has evolved, apparently many times. Both Williams and Hamilton accept that female biased sex ratios in nature are good evidence for group selection on sex ratios.

However, if Wilson and his allies are right, all this is small beer. In the last few decades, evolutionary analyses of social behavior have depended on two central ideas: kin selection is one, evolutionary game theory—most obviously, reciprocal altruism—is the other. Trait group theorists see most of this work as implicitly depending on group selection. So not only are the conditions on group selection less restrictive than had been proposed, but more importantly, mechanisms which all agree are of great importance in social evolution rely on selection between trait groups. Famously, vampire bats share food. These bats die unless they feed every couple of days, and hunting failure is quite common. So food sharing is essential to vampire life. Bats that give are bats that receive. Here too we have a trait group, and the vehicle is the bat population that roosts together. These groups have a common fate. Punishment of defection—of bats that fail to share—suppresses the free-rider problem in ways that parallel the water cricket's clasping adaptation.

If reciprocation is important, kin selection is even more important. The complex social adaptations of honeybees and other highly social insects

[5]Moreover, the formal models often assumed very large within-group fitness differences and relatively weak between-group differences. For altruist groups were able to show the benefits of altruism only in the relatively exceptional circumstances of selfish groups going extinct.

are well-known, and no doubt kin selection has played an important role in their evolution. Kin selection is important not just in these well-known cases. One of their most striking examples is of a parasitic worm (Wilson and Sober, forthcoming). The trematode parasite *Dicrocoelium dendriticum* has a life cycle which takes it through three separate hosts. Adults live in livestock; they lay eggs in the livestock's dung. These eggs are eaten by snails, in whom they hatch and in whom they reproduce asexually for two generations before forming a mucus-covered larval mass which the snail excretes. This mass of several hundred parasites is eaten by ants, the worms' next host. At this stage one of the worm larvae invades the ant's nervous system and changes the ant's behavior so that it spends much of its time on grass tips, thus much increasing the chances that the ant will be eaten along with the grass. Should this happen the brainworm dies, but promotes the completion of the life cycle by the other larvae.

In the picture of evolution informed by trait group selection, the division of organisms into trait-defined groups plays a significant role in the evolution of a wide range of behaviors in many different clades. These theorists do not expect trait group selection to be the only force acting in the evolution of some trait. Often the population of groups will include "mixed" groups, and the outcome will depend on the combination of selection between groups and selection within groups. The view they reject, though, is the idea that we should standardly expect within-group selection to swamp between-group selection.

**3. Reactions to Trait Group Selection.** Trait group selection raises three distinct issues. First, granted that trait groups are important aspects in many evolutionary processes, are trait groups vehicles? An alternative is to think trait groups are a critical part of the environment in which individuals evolve. Second, this possibility raises an overarching question. Is there a single best way of describing these evolutionary episodes (Wilson's way) or, rather, are there a number of equally adequate descriptions of evolution involving trait groups? Dugatkin and Reeve (1994) defend the pluralist idea that there are a number of equally adequate depictions of the trait group phenomena. And third, the pluralist option returns us to the relationship between trait group selection on the one hand and traditional group selection on the other. Wilson and Sober clearly see their work as a partial vindication of the Wynne-Edwards tradition. But that is not obviously so. Wynne-Edwards really did see groups as organism-like. He saw some groups as complex co-adapted wholes. Yet, as we have seen, trait groups need not be much like organisms. The relationship between trait group selection and its ancestors is of more than scholarly interest, for I think that two conceptions of group selection coexist in the

literature, and that trait group evolution characterizes a weaker notion of group selection than "superorganism" evolution.

*3.1 Groups: Vehicle or Environment?* The division of a population into groups surely is important in evolution. But it does not follow that these groups function in ways that parallel the role of organisms. Dugatkin and Reeve argue that there is an alternative account of the evolutionary processes on which Wilson and his allies focus. On this alternative view—"broad individualism"—groups are important aspects of the environment in which selection occurs.

Consider first an example for which the group selectionist perspective is very persuasive. Social insect groups really do seem to be vehicles. They are cohesive, co-adapted, and share a common fate. Ant nests and bee hives seem just as "visible" to selection as individual ants and bees. It is surely just as likely that an ant gene promotes its replication by its effect on an ant nest as on the individual ant in which it resides. Many species of ant have elaborate chemical and behavioral warning and defense mechanisms. Often individual worker's defense chemicals serve a second function of recruiting aid and alerting the nest to danger. Perhaps the genes for these mechanisms replicate via their effects on the nest. Nests with better warning systems last longer and found more colonies, all else being equal, than less efficient nests, and hence the warning genes are preferentially replicated in the ant gene pool.

Even for cases like these, there is an alternative story. Ants carrying the warning gene are fitter in environments in which other ants carry the same gene. In those environments, their signals will attract the appropriate response. Their own responses, too, will be appropriate, for they will not be alone in responding. The close genetic relationship within the nest makes it likely that an ant with the warning gene will be in similar company. So instead of seeing the warning gene as evolving via selection between ant nests we should see it as selection between individual organisms. Ants with the warning gene are fitter, on average, than ants without the warning gene. As always, this fitness advantage depends on the environment in which this evolutionary change is taking place. In this case, a key feature of the environment is the population structure of the ant population itself: the warning gene is fitter only because the population is subdivided into nests each of which consists of close genetic relatives. Nests turn out to be a key feature of the *selective environment*.[6]

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[6]Neander (pers. comm.) has objected that there is an important difference between the defense chemical and an ordinary adaptation. The defense chemical (but not, say, the camouflage stripes on a tiger) only benefits the ant via benefiting the nest. It is only because of the benefit to the ant's nest that ants with defense chemicals are on average fitter. But this response seems to beg the question against the broad individualist by presupposing that nests are vehicles, and have fitness values in the same sense organisms do. Think of any adaptation

A similar line of thought challenges Wilson's and Sober's reinterpretation of kin selection. In environments in which altruists are mostly segregated into groups with others like them, on average altruists will be fitter than defectors, even though the very fittest organisms are the necessarily exceptional free-riders. Again, groups of organisms play a key role as part of the selective environment, not as vehicles of selection. On this way of telling the story, genes for female-biased sex ratios have adaptive consequences for their bearers in certain distinctive social and ecological environments.[7] The moral extends to reciprocation. Instead of thinking that water cricket evolution is driven by group selection, think instead that it is driven by frequency-dependent selection on individual crickets, selection driven by the relative frequency of different types of cricket. Thus the clasping gene is adaptive only when defectors are common. Apparent selection for cooperative groups is selection for cooperative individuals provided there are enough other cooperators in their environment. So group selection is converted into frequency dependent selection on individual organisms.[8] Applying this idea, we could reanalyse the evolution of (say) large flour beetle groups as the evolution of a gene for (say) synchronizing breeding, a gene advantageous only in a particular population-structured context.[9] Once more, groups become part of the selective environment, not the vehicle through which the synchronizing gene ensures its replication.

3.2 One True Story? In his 1987, Maynard Smith suggests that trait group selection is quite often equivalent to broad individualism.[10] He does not think this equivalence is complete, for he thinks that kin selection need not involve a population being segmented into groups. In their 1994, Du-

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that improves the caddis fly larvae's *physical* nest. The broad individualist thinks that the caddis fly larvae is fitter in virtue of that adaptive shift, but not because the nest is a vehicle. The nest is part of the fly's environment, but it is an aspect of the environment in that the fly constructs rather than merely adapts to. That is what the broad individualist says of the *social* nest, too. Nonetheless, I think there is something right about the idea that social insect colonies that genuinely do have fitness properties independent of those of their members, and I will return to this idea in Section 4.

[7] Williams (1992) suggests this line of argument without endorsing it.

[8] Dawkins (1982) sometimes runs a line like this. He recognizes that his conception of the extended phenotype of a gene commits him to the possibility that genes express themselves through group structures. Yet in his 1982 he downplays this possibility; there are passages in which he seems to suggest the appearance of group selection derives from the fact that selective forces acting on individual organisms are sensitive to the social environment of those organisms (1982, 240–241).

[9] Synchronized breeding seems important in the evolution of large flour beetle groups in the Wade experiments, because it cuts down on cannibalism.

[10] Broad individualism, in turn, he thinks has several equivalent formulations. Sterelny and Kitcher (1988) and Waters (1991) also defend "pluralist" interpretations of evolutionary theory, though their focus is gene *vs.* individual organism selection, not group selection.

gatkin and Reeve go the whole hog in defending pluralism. They do not claim that broad individualism is the right picture and trait group selection wrong. Rather, they argue that each is equally good; we have two equivalent descriptions of (say) the evolution of honey bee altruism. On only one the colony counts as a vehicle. On this view, while the caste of replicators is an objective feature of the history of life, the caste of vehicles is not. There is no fact of the matter as to whether a vampire pair that shares blood is really a vehicle of selection or not. There can, however, be heuristic differences between the two approaches. So the vehicles we should recognize depends on our explanatory and predictive interests.

A similar moral emerges from one way of reading Dawkins' reaction to trait group selection. Dawkins (1982) defends the idea of the "extended phenotype". Genes have effects that promote their own replication but which are not expressed as traits of the organism in which they ride. So extended phenotype genes are active replicators, but not replicators that compete with their rivals by constructing vehicles. Genes that code for kin selected traits and reciprocation are genes with extended phenotypic effects. So Dawkins (1994) rejects the idea that kin groups and reciprocation groups are vehicles. But instead of accepting broad individualism he argues that in the evolution of water cricket navigation there is no vehicle at all.

Amongst Dawkins' most striking examples are parasite gene effects expressed as host behaviors, and this raises the possibility that trematode altruism is a consequence of the manipulation by genes in other larvae. Perhaps there is a trematode arms race, with all the larvae exuding both "turn into brainworm" signals aimed at their fellows, and smokescreens to protect themselves. The brainworm is the first larvae whose defenses are swamped. If this is the mechanism, it would look a lot less like altruism. Let us assume though that the transformation into a brainworm is not the result of loss in an arms race. If so, one might think of trematode parasite *Dicrocoelium dendriticum* as having evolved a lottery gene. Trematodes with this gene take part in a lottery. If they lose the lottery, they become the brainworm and die. If they win, they are in a group in which another trematode transforms itself into a brain worm, and they have a much increased chance of completing their life cycle. The lottery gene has better replication prospects than its rival if either the chances of trematode's chances of completing its life cycle without the intervention of a brain worm are very grim (for then you have little to lose by entering the lottery), or if many of your companions have also entered the lottery, thus reducing your chances of losing. Lottery genes of this kind seem quite common. For example, in times of scarcity slime molds aggregate to a single multicelled fruiting body in which reproduction is a lottery. Cells at the tip of the body form spores, but those that form the supporting structure have lost the lottery and forgone their chances of reproduction.

What are the phenotypic effects of lottery genes? What is the adaptation in virtue of which they improve their replication prospects? Dawkins' point is that we are not compelled to nominate a vehicle as the bearer of an adaptation. Not all evolutionary processes involve vehicles. In the introduction of his 1982, he defends a pluralism not unlike that of Dugatkin and Reeve. So one could read this alternative in a modest way, arguing, with Dugatkin and Reeve, that the Wilsonian examples can be as well described from the perspective of gene's extended phenotypes; we have an adequate vehicle-free description of these examples.

Wilson and Sober, not surprisingly, are rather skeptical of pluralist responses to trait group selection. I take their skepticism to have three central elements. First, they suspect a fudging of the issues is in the air. After all, it cannot be the case *both* that Maynard Smith, Williams, and Hamilton refuted group selection *and* that group selection is really, in the end, just a version of standard Darwinian individual selection. I think this is right. We should regard broad individualism (and even more Dawkins' conception of selection without vehicles) as an important shift in our conception of evolution rather than a vindication of the 1966 status quo. It is a shift that recognizes the importance of social environment and population structure in behavioral evolution.

Second, they suspect that individualist redescriptions involve an "averaging fallacy." Suppose that the cooperative dam building is evolving in a beaver population because the boost to beaver productivity in well-maintained dams outweighs the cost of free-riding in mixed groups. The averaging fallacy just averages the fitness of cooperators in all the groups in which they exist and compares them to the defectors. In our scenario the productivity boost in cooperative ponds leaves the average cooperative beaver fitter than the average non-builder. Hence cooperation evolves because the individual organism is fitter in virtue of being cooperative. In effect, the average fitness figures for cooperation and defection sum the results of all these selective processes to yield the result of selection. The process of averaging bleaches out all the information about process, all information about the mechanism or mechanisms in virtue of which the cooperating beaver is fitter than its rival. There is surely much justice in regarding this as a very misleading picture of the evolution of cooperation. Hence Wilson and Sober think of "broad individual" selection as trivializing the idea that the individual organism is the vehicle of selection.

The proper conception of an evolutionary change must retain information about the process of that change, and should not just report an average result. But there is a way of understanding "broad individual" selection so that it does not merely average the fitness of every type. Let us suppose that female lioness's tolerance of one another's cubs suckling has evolved by kin selection. On the trait group conception, the greater

fitness of suckling-tolerant groups outweighs the within-group fitness ad-
vantage of free-riding. There is an alternative story here that does not
commit the "averaging fallacy." A broad individualist says that the fitness
of individuals in the groups with (many) altruists is higher than the fitness
of the individuals in the selfish groups. On this reformulation, the broad
individualist recognizes that two elements combine to explain an organ-
ism's fitness: the contribution to the fitness the organism has from being
in a group of a certain kind and the contribution from its role in that
group. The fitness of groups drops out.

   On one view, suckling tolerance evolves because suckling tolerant
groups are more productive; sufficiently so to outweigh individual selec-
tion for suckling intolerance. On the other, the average suckling tolerant
lioness is fitter than intolerant lionesses, because she is likely to live in
suckling tolerant groups, and despite the fact that her behavior in that
group does not give her any relative advantage over her pride-mates. In-
tolerant lionesses' fitnesses are not depressed by the role they play in their
prides. But since most live with equally mean sisters, their average fitness
is depressed by the character of their social environment, despite the fact
that the necessarily rare intolerant females in tolerant prides do best of
all. Since both pictures recognize the importance of the division of the
population structure into prides, and recognize that an organism's fitness
depends both on the character of the group it inhabits and its character
in that group, it is surely very tempting to agree with Dugatkin and Reeve:
these pictures are equivalent. Defenders of the "extended phenotype" may
exploit the same idea. So long as the replication potential of the gene
depends both on it place in the meta-population of genes and its role in
the local population, no averaging fallacy is committed.[11]

   Third, Wilson and Sober argue that the conception of trait group evo-
lution "also predicts that natural selection can operate on units that were
never anticipated by kin selection and game theory, such as multi-gener-
ational groups founded by a few individuals . . . and even multi-species
communities." (1994, 597) This suggestion does highlight something of
profound importance, easily overlooked by those in the grip of the stan-
dard picture of kin selection: trait group population structure can be of
profound evolutionary significance independently of considerations of

   [11]Paul Griffiths has suggested (pers. comm.) that this conception of an organism's fitness
as having two sources may understate the complexity of real selection processes. We know
that there can be very complex many-one relations between evolutionary shifts at the level
of genes and at the level of the phenotypes those genes express. A simple phenotypic shift
can conceal complex genotypic shifts. Equally, perhaps simple shifts in the nature of trait
groups may depend on very complex shifts in the fitness of the component organisms; shifts
whose complexity is not captured by the simple dichotomy of fitness from within group, and
fitness from the nature of the group. Perhaps so, but then the same problem is an objection
to the trait group model. For it too trades in only two fitness commodities: the fitness of
trait groups and the fitness of individual members of those groups.

kinship, for the fitness effects on an individual of trait group membership depend only on variance between trait groups, not on the mechanisms which cause that variance. However recognizing the contribution to an organism's fitness deriving from its place in this population structure does not require us to conceive of trait groups as vehicles.

So Wilson's and Sober's reasons for rejecting pluralism are not convincing. Moreover, pluralism mitigates a serious objection to the "trait group" analysis. The canonical examples of trait groups often do seem like high level vehicles. Ant colonies and vampire bat roosts are not theorists' inventions but parts of the biological landscape. But these examples make it easy to overlook how many populations emerge as structured into trait groups on their analysis. These include cases which do not seem like the selection of groups at all. If one were to insist that the trait group description of these cases is the only correct description, and that trait groups are high level vehicles, then these cases emerge as important counterexamples.

Trait groups are linked by their "common fate." But what is common fate? Our trematode parasites might be thought to share a common fate, in a certain Irish kind of way. Even though one dies in the ant to send her fellows to the cow, all enter the brainworm lottery and that is their common fate. But some of the examples of Wilson and Sober 1994 trade on a still more attenuated conception. To bring evolutionary games theory within the trait group ambit, they need a very inclusive sense of "common fate." Recall the water crickets; on their view, improved coordination evolves by selection of trait groups consisting of the boating pair, for the better coordinated cricket "can evolve only by causing pairs to succeed relative to other pairs" (1994, 596). Despite their ephemeral nature, the two crickets boating together have a common fate. So Wilson and Sober treat the pairs as groups with a fitness value even when thinking of the evolution of defection (1994, 597). So on their view, the pair consisting of a naive cricket and a partner that drowns him is a vehicle with low fitness. But surely there is no sense in which the defector and its victim have a common fate in virtue of their shared journey across the pool.

Other examples that make the same point. The fictional Greenbeard Gene has enjoyed a modest fame in the evolutionary literature. Carriers of the Greenbeard gene (a) have Greenbeards and (b) aid other Greenbearded organisms. Now Greenbeard Genes have often been taken to be outlaws. The paradigm outlaws are meiotic drive genes which undercut the fitness of the organism they inhabit as a consequence of their biasing their prospects of reaching the gametes. Similarly, Greenbeard genes sacrifice the interests of the organism they inhabit to help copies of themselves in other organisms. Yet on Wilson's account, the Greenbeards are a trait group. The Greenbeard trait cuts out a sphere of influence: the organisms

that are the potential beneficiaries of the organism carrying the "sacrifice yourself for the Greenbeards" trait. If the Greenbearded gene increases in frequency as a result of mutual aid, it does so by group selection. It is surely very weird to interpret the evolution of an outlaw gene—if Greenbeards really are outlaws—as group selection.

The outlaw status of the Greenbeard Gene is controversial. But uncontroversial examples of outlaws look like examples of trait group selection, too. In his 1982, Dawkins imagines a male outlaw gene. His outlaw is a gene on the Y chromosome that biases its male carriers towards his sons, and hence towards copies of the male bias gene. The imagined male feeds his daughters to his sons. By Wilson's definition, the "cannibal-Y" males in a family will form a trait group—an exotic kin group—and if the "cannibal-Y" gene evolves, it will evolve by boosting the output of the cannibal-Y group, and it will evolve despite the fact that cannibal-Y males are less fit than normal males which have both sons and daughters that survive and reproduce. This is very paradoxical. Outlaws are ultraselfish genes. They are genes that become more frequent in virtue of evolution below, not above, the level of the organism.

So if Wilson, Sober and other defenders of trait group selection insist that trait groups are real units of selection, we seem here to have a series of examples that argue that their conception of common fate is too weak, and interactions between trait group members too varied, for every trait group to count as a vehicle. On the other hand, if we see the trait group analysis of these cases as an often useful heuristic, but one of several, then the fact that some of these cases do not look like examples of high level groups is no longer a problem.

This idea is reinforced in other ways. Maynard Smith (1987, pers. comm.) denies that kin selection *requires* a population divided into groups. He invites us to imagine a forest consisting of a pure stand of a single species. If seed dispersal is limited, distance in space will vary pretty smoothly with degree of relatedness, so neighbors will be relatives. Altruism might evolve. Of course, we *can* construe this as a population divided into groups. So, for example, we can pick a set of focal individuals, and construct our groups around these, treating (say) the ten nearest neighbors of each focal individual, plus that individual, as a group. We would thus conceive of our forest as a patchwork. Within each group a defector (say a tree that hogs the light) will do better than an altruist. But still, altruist groups might be productive enough overall for the average altruist to do better than the average light hog. The problem, though, is that the patchwork is arbitrary; there are many different, equally good, ways of constructing our patchwork.

The moral is the same. We should think of the trait group conception as a good heuristic for thinking about kin selection and social evolution

more generally, but we should not think of it as the only correct view of these evolutionary episodes.

*3.3 Group Selection: Old and New.* I think the pluralist suggestion of Dugatkin and Reeve hints at an important discontinuity between old style group selection and trait group selection. An organism, as the trait group theorists frequently remark, is a population of cells. So do we have two equivalent, equally good descriptions of the evolution of some paradigmatic adaptation of an individual organism? One would speak of the relative fitness of individual organism. The other would identify the individual cells as vehicles, and recognize two vectors in their fitness: a fitness component from their role within the population of cells that the vulgar think of as an organism, and the fitness they derive from the character of that population *vis-à-vis* other populations? This generalized version of broad individualism fails to recognize the importance in evolution of the organism. The idea of the vehicle recognizes and identifies the organism's role, but only if the evolution of the vehicle is an objective feature of evolutionary history. The same, arguably, is true of other highly co-adapted populations: termite nests, ant colonies and the like.

This contrast in examples suggests that there is lurking ambiguity in the group selection debate. One strand of this debate is the attempt to characterize *population structured selection*. These form the central pool of examples of those who defend trait group selection. My suggestion, paralleling Dugatkin and Reeve, is that trait group selection, broad individualism, and extended phenotype theory all give equivalent formulations of population-structured selection. Population-structured selection is a precondition for the evolution of high level vehicles, and the evolution of population adaptations. For want of a better term, I will refer to this stronger sense of high level selection as *superorganism selection*. This ambiguity is reflected in the history of the debate. Old style group selectionists (especially those whose paradigm was the social insect colony) often seem to have something like the superorganism in mind, for they emphasized the integration and cohesiveness—the organism-like characters—of their collectives.[12]

Wilson and Sober are friends of the superorganism but do not think there is a distinction *in kind* between superorganisms and lioness kin groups, lion coalitions, or water cricket pairs. Our trait group becomes more like a superorganism to the extent that fitness differences within the group disappear (1989). The clasping adaptation, on this view, pushes water cricket evolution towards the superorganism end of the continuum

[12]Though as Wilson has pointed out to me, quite often this does not seem to move beyond rhetoric. Their models have been, like the trait group theorists', models of the evolution of particular traits.

for it suppresses within-pair differences.[13] Their 1994 paper supplements this criterion with a second. Trait groups become more like organisms to the extent that different trait groups pick out the same creatures. On this view, there is no qualitative distinction to be drawn between water crickets, lion coalitions, and social insect nests.

Though of course there will be borderline cases, I suggest the distinctions between population-structured selection and superorganism selection are quite robust. Where we just have population-structured selection, we have "mere" trait groups. We can see these as vehicles, but there are equally adequate alternatives that do not so conceive of them. But population-structured selection occasionally leads to the evolution of superorganisms, organizations of organisms which have as good a claim to being objective vehicles as organisms themselves. In the final section, I explore some differences between trait groups and superorganisms.

**4. Real Vehicles.** I think there are two ways in which we might distinguish trait groups from superorganisms. The first focuses on the fitness of the composition, and on whether it can vary independently of the fitness of the components. The other argues for the importance of cohesion.

*4.1 Trait Group Fitness and Organism Fitness.* In the last section, I sketched the broad individualism of Dugatkin and Reeve, and showed that the broad individualist can redescribe even some social insect evolution as population-structured evolution. However, the example I discussed had a rather special feature, one which makes this redescription especially plausible. The trait group story, the extended phenotype story, and the broad individualist story all identify the same adaptation. The relevant chemical products evolve through their function in warning and defense, whether we see this as an adaptation of the nest, the ant, or the genes. Similarly, we see the clasping gene as adaptive because it prevents a cricket's partner from leaving the leaf first, whether or not we think of the cricket pair as the vehicle of selection or as part of the environment.

There are examples which suggest that the fitness of the nest is not just a simple sum of the fitness of the individual organisms within it, for it can vary independently of those organisms' fitness values. In these cases, broad individualist and trait group models identify distinct adaptive effects. So counterfactual scenarios and comparative biology can discriminate between hypotheses in which the nest is the vehicle, and those in which it is

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[13]Perhaps not very far. For the clasping adaptation may well not be the end of the defection/cooperation arms race. One might well read Wilson and Sober as thinking that superorganisms have evolved only when fitness differences within the trait group have gone for good. We have a superorganism when the component organisms are in a fitness-equalizing evolutionary sink—when, in Dennett's terms, their commitment to their fellows is ballistic, not up for renegotiation (Dennett 1994).

the environment. For example, in some eusocial insect species, there are genes for sororicide. In single queen colonies, when a new generation of queens hatch, the first hatched kills potential rivals. Consider the sororicide gene, and its actual and potential rivals. There are (at least) two possible mechanisms by which this gene might compete with its rivals. These mechanisms identify distinct adaptations conferring fitness benefits on different vehicles.

One idea is that this gene adapts the nest itself, by decreasing genetic variation with the nest. Hence it helps to suppress destabilizing within-nest competition. The idea is exported from Buss (1987), who demonstrated that the genetic uniformity of individual organisms is no accident.[14] There are many mechanisms that function to suppress genetically distinct cell lineages within organisms, for such lineages have the potential to subvert the integrity of the organism. Presumably, the same is true of nests: the more genetically heterogeneous a colony, the greater the potential for within-colony conflict. So selection between colonies would favor variation which resulted in greater homogeneity.

The organism level hypothesis about sister-killing sees it arising through a prisoner's dilemma. Once the sororicide gene appears it will spread, even if it were from the perspective of the nest an outlaw. It is an organism-level equivalent of a meiotic drive gene. In an environment in which your nest mates are likely to carry the sororicide gene, you will be very unfit unless you carry it too. So though it increases the genetic homogeneity of the nest, that is a side effect of the organism-level prisoner's dilemma.

These adaptive ideas are not equivalent, for we can envisage one component of the environment changing without the other varying.[15] So consider counterfactuals in which we vary the individual consequences of sister-killing. In nests in which workers protect queens that do not strike first, the prisoner's dilemma is suspended. That is equally the case if royal eggs hatch in separate parts of the nest, so queen hatchlings can avoid their sisters. In such environments, whether or not uniformity is a nest level advantage, the prisoner's dilemma hypothesis says we should not find sister-killing.

Next consider counterfactuals in which the prisoner's dilemma still

[14]Genetic diversity within the one organism signals potential conflicts of interest, but that potential is mostly blocked by mechanisms that ensure that no DNA in a given organism can replicate except by aiding the replication of other DNA. Hence the germline DNA has a common fate. This connects importantly to Dawkins' conception of an organism as defined by the developmental cycle. For if there were no developmental cycle, we should not expect fate to be common: the way would be open for distinct cell lineage to control different avenues of reproduction, and hence common fate would be undermined.

[15]I think the suggestion here is an informal equivalent of the criterion on high level selection run by Lloyd (1988), and Damuth and Heisler (1988) who define high level selection by appealing to the irreducibility of the fitness of high level interactors to the fitness of lower level interactors.

rages, but without the nest level consequences we have been considering. Think of nests in which a single queen has many suitors, or nests in which queen generations overlap. In such circumstances, sister-killing would not lead to genetic uniformity. In these counterfactuals, we consider worlds in which the trait does not have the same effect on nests as it does in our world. In these worlds, there is no between-colony selection for sister-killing, so if the "unity of the nest" hypotheses were right, these worlds would not be sister-killing worlds. Comparative biology may provide a reasonable analog of these possible worlds. For example, we could hope to confirm a "unity of the nest" hypotheses by showing that we have sister-killing *only* when it generates genetic uniformity.

Nests and hives are very plausible examples of real vehicles. So it is not surprising that there are at least some hypotheses about nest adaptation which do not translate smoothly into hypotheses about individual organism adaptation. We could see warning either as advantageous for the ant, in the right social circumstances, or as advantageous for the ant nest. But if we have the adaptive mechanism of sister-killing right, the same double vision for it is not so plausible. We cannot see it as good for the sister-killers, given the fitness contribution from their social environment, or good for the hive, while focusing on the same set of causal interactions. If it is a winner-take-all prisoner's dilemma, it is mandatory for the sister-killers irrespective of the fitness consequences for them of their more genetically uniform world. If it is a consequence of hive level selection for genetic uniformity, then the sister-killers have entered a lottery altruistically. For the bee sister lottery is unlike like the brainworm's lottery, where each entrant had so much to gain and a much smaller risk. Hence we could see the brainworm lottery both ways. But if we set aside the prisoner's dilemma, it is hard to see that the bee sisters are individually better off by entering such a fatal lottery.

Let me try to make vivid the relative independence of hive fitness and organism fitness in a slightly different way. I have been considering thought experiments to pry apart hypotheses about social insect groups from hypotheses about their members. We cannot run analogous thought experiments about our water crickets and the water cricket pair. The "fitness" of the pair just is the fitness of the individuals in the pair. Knowing the fitness consequences for the interaction for each member of the pair just is knowing the fitness of the pair. It is just a simple sum of their fitness, so we cannot envisage counterfactuals in which the two come apart. The values cannot vary independently. Knowing the fitness consequences for each individual lioness, of tolerating or failing to tolerate suckling, just is knowing the fitness consequences for the pride of that trait. To know whether suckling tolerance will evolve, we need of course to know the fitness of other prides as well. But the fitness of each pride member specifies

the fitness of the pride. But if sister-killing improves the prospects for the hive's survival, and its prospects for founding new colonies, knowing the fitness consequence for each would-be queen of their deadly interaction is not knowing the fitness consequence of that interaction for the hive. As we shift from superorganisms to organisms themselves, this information gap becomes still clearer. Knowing the reproductive fate of a given cell lineage (or even all of them) will often tell you very little about the fitness of the organism.

*4.2 Vehicles and Their Environment.* In the eyes of Dawkins, Hull, Buss, Wilson, Sober, and others, organisms are exceptional products of evolution. For Dawkins the vehicle is a *special case* of interaction. Sometimes the adaptive phenotypic effects of genes combine together in the design of a single structure in which they reside. Then and only then we have a vehicle. When adaptive phenotypic effects come bundled together in a single integrated entity, we have a natural segmentation of an evolutionary process. It divides into the adaptations genes code for versus the environment in virtue of which those gene effects are adaptive. There is no greater difficulty in segmenting ant nest from ant environment than there is for doing the same with the individual ant, for ant nests, too, are integrated and cohesive.[16] It is perhaps for this reason that Hull, despite the generality of his aims, defines interactors as units that interact with their environment as a cohesive whole. Interactors are structured units, units with effects on one another, effects with downstream consequences on replication propensities.

Once one moves away from the insistence on interactors as complex wholes, the robust distinction between adaptation and environment comes under threat. So, for example, we can "move the boundaries" with Dawkins' "Extended Phenotype" examples. For example, we can take the adaptive effect of the Bruce Effect abortion genes to be that of causing newly pregnant females to abort in an environment in which he is a potential father when she comes back into season. Alternatively, we can take it to be the production of the abortifacient pheromone. That pheromone is adaptive in an environment in which newly pregnant females lack chemical protection for such pheromones and in which he is her potential mate. So Dawkins says:

> Whichever link in the chain a geneticist chooses to regard as the "phenotype" of interest, he knows that the decision was an arbitrary

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[16]Though the genotype/phenotype relation is different in superorganisms than organisms. Migration in and out of a superorganism, and deaths of component organisms and their genes, imply that genetic inheritance in superorganisms can be Lamarckian. A phenotypic change can cause a genetic change in a superorganism—a loss or gain of an important gene— which is inherited to the next superorganism.

one. He might have chosen an earlier stage, and he might have chosen
a later one. So, a student of the genetics of the Bruce Effect could
assay male pheromones. . . .Or he could look further back in the
chain. . . .Or he could look later in the chain.

What is the next later link in the chain after the male pheromone?
It is outside the male body. . . .He chooses for convenience to end his
conceptual chain at the point where the gene causes pregnancy block-
age in females. That is the phenotype gene product which he finds
most easy to assay, and it is the phenotype which is of direct interest
to him as a student of adaptation in nature. (1982, 230)

The idea of the extended phenotype subverts the idea that genes always
combine to operate on the environment as a cohesive whole. We can draw
a clear distinction between adaptive trait and the selective environment in
virtue of which a trait is adaptive only when phenotypic effects are bundled
into vehicles rather than dispersed as interaction. Kin groups and tem-
porary coalitions do not have determinate phenotypes. They do not allow
an objective distinction between their design and the environment in virtue
of which they are designed. So they are not "real vehicles."

Wilson and Sober resist the idea that vehicles must be cohesive and
integrated. But dispersed and uncohesive "quasi-vehicles" have neither
physical nor functional boundaries. I doubt that there is a clear way of
distinguishing between a quasi-vehicle and its environment. That is why
we can reinterpret trait group selection as selection of individuals in a
particular population structure. I see three possible lines on the boundary
issue:

    (a)  We could attempt to defend an objective way of drawing the ve-
hicle/environment boundary, even for unbundled effects empha-
sized by Dawkins, Wilson, and Sober.

    (b)  We might accept that when, but only when, the phenotypic power
of a replicator is unified into a vehicle, there is an objective dis-
tinction between adaptation and environment.

    (c)  We might read the arbitrariness problem back into the cases
where we have vehicles. Even when we can identify an organism,
or something like an organism, there is no objective way of dis-
tinguishing between adaptation and environment.

The trait/environment distinction would be unproblematic if we could
appeal to development to distinguish adaptation from environment. But
it is most unlikely that the causal histories of, on the one hand, water
cricket cooperation and, on the other, the environmental structures that
make that cooperation adaptive divide neatly into different kinds. It would
be unproblematic if we could see selection as adapting a population to its
environment. For then adaptive phenotypic effects would be evolution-

arily labile, whereas the selective environment would be fixed. Relative stability would distinguish world from design. But this picture of evolution breaks down in contexts in which the social environment is salient in selection. For then population and environment change together.

Wilson and Sober think that the trait group selection reading of water cricket evolution is right, and the broad individualist version wrong. So they are committed to (a), a general objective distinction between adaptive effects and the environment in virtue of which those effects are adaptive. It is hard to see how to sustain that distinction. If that is right, there really is a qualitative change in the shift from population-structured evolution to superorganism evolution. Cohesion matters. Organisms and superorganisms are real vehicles. There is a fairly objective description of their location in design space. Their existence and location in the biological world is stance-independent. Trait groups that are not cohesive do not share this objective existence as vehicles.

**5. Conclusion.** I have not traveled all the way with Wilson and his allies in their revival of group selection. But that skepticism should not obscure the importance of their reinterpretation of social evolution. First, they are right to emphasize the great importance of population-structured evolution. It has a pervasive role in evolution. Moreover, while it is not compulsory to view the process as group selection, it is a striking fact that their picture is often a very intuitive conception of many of these episodes. Second, they are right, I think, to decouple population-structured evolution from kin selection. Relatedness is one mechanism—perhaps very important, but still only one mechanism—that generates important structure in the population. Third, they are right to insist that our conception of evolution be sensitive to the mechanism of evolution, not just its output. Finally, they have helped identify a mechanism that can lead to real high level vehicles.

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