entire species. The units-of-selection controversy concerns levels of interaction, not levels of replication. However, to use the ambiguous term "selection" to characterize this controversy is to ask for continued misunderstanding.

In addition, I think that my concept of an interactor makes for a better restructuring of selection than does vehicle; but the term itself is also preferable, because "vehicle" has all sorts of misleading connotations (Brandon & Burian 1984, Eldredge & Grene 1992; Williams 1985; 1992): It implies hapless robots being controlled by all-powerful genes. Although this characterization may fit the entities that function in certain selection processes, it does not accurately characterize the entities that function in all selection processes. For example, demes may well function as interactors. They are in no sense "lumbering robots." Although colorful metaphors make for interesting reading, they have their costs as well. "Vehicles of selection" trips off the tongue all too misleadingly, unlike "interactors of selection."

Different vehicles for group selection in humans

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Abstract: Two vehicles for group selection may have selected for distinctly different traits in humans. Twenty-five member hunter-gatherer groups would have selected for altruism toward known group members. Village and tribal groups (250+ persons) would have selected for outgroup competitiveness. Neither would select for altruism toward strangers.

I strongly agree with Wilson & Sober's (W & S's) assertion that principles of group selection can be applied to human evolution. I disagree with the specific way in which that application is made because it fails to take into account the social context in which prehistoric people lived. Human social evolution has involved increases in group size, and groups of different sizes are vehicles that may have selected for different psychological traits.

For 90% of the time that anatomically modern humans have existed on this planet they lived in hunter-gatherer groups of about 25 persons, who, by inference from recent hunter-gatherer groups, were able to survive because of considerable cooperative skills (Gamble 1986; Geist 1978). Many recent hunter-gatherer groups have shared ownership of property (Service 1966) and are similar in this respect to the Hutterites. Previous hominid forms probably had simpler but nevertheless cooperative social structures. That archaic hunter-gatherer groups survived owing to cooperation has been used to explain the evolution of the trait of altruism (e.g., Caporael et al. 1989). However, the English language fails to distinguish two different forms of altruism. Altruism$_1$ occurs when one person is altruistic toward an unknown other: this is the type of altruism that may be observed in the prisoner's dilemma game and is illustrated by the parable of the Good Samaritan. Altruism$_2$ occurs when one person is altruistic to another who is known and loved. Inference from archaeological data suggests that Upper Paleolithic groups were characterised by strong emotional bonds, which would have enhanced the cooperation and altruism$_2$ necessary for survival. Given the very low population density of archaic humans it is unlikely that there would have been much opportunity for altruism$_1$, and although it is possible to envisage scenarios where altruism$_1$ would have been advantageous (e.g., giving support to another group when their prediction of animal migration failed), there is no clear evidence that this was the case.

W & S, like others before them (e.g., Caporael et al. 1989), link the altruism$_1$ found in the prisoner's dilemma game or in religious beliefs to human evolution, but this is not justified from archaic human society. Indeed, a primary objective of the prisoner's dilemma and other game theoretic paradigms is to select individuals who do not know each other so that the results are not affected by the emotional ties between them – ties which might otherwise increase the likelihood of cooperative strategies. Religions advocating altruism$_1$, such as Christianity, had an impact 2,000 years ago because they promoted altruism$_1$ when this was not an accepted philosophy (Ling 1968). It is of course possible that altruism$_1$ is the consequence of generalization of altruism$_2$ (loved ones and strangers share human features), or it may be that the philosophical principles of altruism$_1$ have developed independently of evolution. Nevertheless, although the parliament of a religious order that requires altruism$_1$ may have rules similar to those that suppress traits adaptive at an individualistic level, the evolutionary evidence does not provide any clear support for the hypothesis that altruism$_1$ had a positive influence on group survival. By contrast, the trait of altruism$_2$ can be explained in terms of group selection because it would have supported archaic hunter-gatherer survival. Altruism$_2$ arises from strong emotional attachments (also called "love") to familiar family and nonfamily members. (Attachments to the latter have recently been "rediscovered" as male and female bonding.)

Approximately 10% of anatomically modern human existence has been spent after the agricultural revolution when group sizes (i.e., villages, towns, cities) were often in excess of 250 people. From the Neolithic period onward, there is evidence of warfare between people as groups competed for scarce resources. It is possible that traits became selected even at this late period in human evolution, and if that were the case, the vehicle of selection would not be the 25-person group, but the 250$^+$-person tribe/nation. When populations compete with each other, traits favoring outgroup discrimination are advantageous. Far from expecting the selection of altruism$_1$, a social context of warfare favors the development of aggressive competitive tendencies where harm of unknown others is actively sought. The historical record shows that warfare and genocide have been and are common. Whether competitive traits have become selected after less than 10,000 years, which is only a short period in evolutionary development, is unknown. Farming was invented earlier in the Old World than the New World, so competitiveness would have had longer to evolve there. The greater dominance of Old World people throughout the world may not, however, be the result of a greater propensity for warfare and genocide but may simply reflect better skills at warfare.

W & S distinguish group-level from metapopulation-level selection, a useful distinction for understanding human evolution as societal structures changed during human prehistory. Small, sparsely distributed hunter-gatherer groups would have favored the trait of altruism$_2$. Wealth-owning, farming communities would have favored traits of competitiveness toward strangers but would not have selected against altruism$_2$. Altruism$_1$ certainly exists, as examples cited by W & S show, but it is not easy to see how altruism$_1$ evolved on the basis of the vehicles available for human group selection.

Rx: Distinguish group selection from group adaptation

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I admire Wilson & Sober's (W & S's) aim, to alert social scientists that group selection has risen from the ashes, and to explicate its relevance to the behavioral sciences. Group selection *has* been

widely misunderstood; furthermore, both authors have been instrumental in illuminating conceptual problems surrounding higher-level selection. Still, I find that this target article muddies the waters, primarily through its shifting and confused definition of a "vehicle" of selection.

The fundamental problem is an ambiguity in the definition of "adaptation." On the one hand, any evolutionary change that *results* from a selection process could be called an adaptation, by definition; I call this the "weak" view of adaptation. A "strong" view of adaptation, on the other hand, includes some notion of *design* – the evolution of a specific complex trait understood, in an engineering sense, to provide a mechanism favoring its owner's success in contributing to the evolutionary lineage.

I have analyzed various units of selection problems by distinguishing four discrete roles: *interactor, owner-of-adaptation* (in the strong sense); *replicator* (now *reproducer*, see J. Griesemer 1994a; 1994b); and *beneficiary* of a selection process. Quite a bit of the heat in the group (and species) selection debates over the past three decades has been generated precisely by the authors' implicitly defining a "unit of selection" as different *combinations* of the four roles (Hull 1980; Lloyd 1988; 1989; 1992; Lloyd & Gould 1993).

W & S present themselves as arguing against Williams's (1966), view which explicitly concerned "group-level adaptations" (pp. 3, 5, 6). They do not emphasize, however, that Williams's primary concern, like Maynard Smiths's, Dawkins's and others was whether *strong adaptations at the group level* are produced by processes in which the groups are interactors. Technically, this should have been called "(strong) adaptation by group selection." It is true that Williams (1966) equated group selection with group ownership of adaptations in the strong sense, though he no longer does (1992, pp. 26–27). Similarly, Maynard Smith was arguing against adaptation by group selection, not against the evolutionary impact of groups as interactors, *simpliciter*. In 1987, though, Maynard Smith explicitly recognized that adaptation by group selection is *different* from group-selection processes where groups are functioning, evolutionarily, as interactors (1987a, p. 123). Cronin (1991) also recognizes this distinction, in the form of her "strong" and "weak" group selection; she is very clear about denying *only* the group adaptation by group-selection process – that is, she is interested in units of selection that are *both* interactors *and* owners-of-adaptations (cf. Lloyd 1988). Yet W & S seem to have rejected the significance of these recent distinctions in the very authors they criticize.

The primary problem – and it is a significant one –with W & S's account is that they seem to hold a *variety* of views about what a "vehicle" is. They do give a rule of thumb for identifying "vehicles," on p. 9. I find most of this indistinguishable from my own definition of an interactor (1986; 1988), which was, in turn, extracted and revised from Wimsatt's definition (1980; 1981). The only difference I can see between W & S's definition and my own is that theirs is vaguer, and potentially misleading: (1) they do not emphasize that the attribution of being a higher-level interactor involves examining the population and fitness structure of at least two levels; (2) their definition is in terms of genes rather than genotypes, contrary to population genetics group-selection models (Cavalli-Sforza & Feldman 1978; Mueller & Feldman 1985; Uyenoyama & Feldman 1981); and (3) their definition includes a clause at the end that seems to equate being an interactor with having a "functional organization," which later seems to be identified as a strong adaptation. Yet their own rule of thumb will pick out only higher level traits that are *selected* at that level, *not* those that are functional adaptations in the strong sense.

If W & S held a weak view of adaptation, then the identification of something as an interactor would be enough to claim that the trait-in-play was an adaptation. Unfortunately, they seem instead to adopt a strong view of adaptation; they further confuse the issue by referring to "functionally-organized," "adapted" entities as *organisms* (p. 18). Being an *organism* (also called "vehicle") includes *being an interactor* and *being an owner-of-an-adaptation* in the strong sense (p. 20). Later, it also includes *being a beneficiary* of a selection process.

The problem is that their method for identifying vehicles picks out only *interactors* – they use "fitness effects" to identify "the vehicles that natural selection acts upon." But I gather that W & S are after *more* than interactors, because they say that Gould's (1992) definition of vehicle differs from theirs, and that the concept of species selection he "emphasizes" is different from their concept of group selection. I would agree, because Gould explicitly uses my distinction between being an interactor and possessing a strong adaptation at that level. Williams has also accepted my distinction between interactor and owner-of-adaptation in species selection (1992, p. 27).

In sum, W & S have offered a shifting definition of "vehicle" that sometimes means simply *interactor*, sometimes *owner-of-adaptation* as well in the design sense, and sometimes even *beneficiary* of the selection process. Furthermore, they have adopted a method for identifying "vehicles" that has been defended elsewhere as appropriate only for identifying *interactors*. They also have missed the pivotal point of disagreement among most of the authors they cite, which revolves, not around the role of genes in selection processes, but around the definition of *adaptation* itself, and whether natural selection processes at a given level are properly interpreted as necessary *and sufficient for* the evolution of "adaptations" at that level.

We are left confused rather than enlightened. Still, I hope that Wilson & Sober's target article will succeed in raising the awareness of the importance of group selection in evolutionary biology today, and will prompt other researchers to investigate these issues further.

Group evolutionary strategies: Dimensions and mechanisms

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Wilson & Sober (W & S) make a major contribution by developing the vehicle concept as a general rubric for thinking about levels of adaptation. The greatest impact of the target article will be to counteract what has become virtually an *a priori* assumption among evolutionists: that human groups must be understood atomistically as composed of individuals striving to increase their inclusive fitness; and the correlative assumption that groups are an unnecessary level of analysis. For example, the unstated assumption of Alexander's (1979) and Betzig's (1986; 1992) work on monogamy is that wealthy and powerful males are always able to maximize their reproductive success.

The implication of W & S's work however, is that social controls and ideologies acting within the group may serve to structure reproductive opportunities, with the result that there is no theoretical reason to suppose that wealthy and powerful individuals will always maximize their individual fitness. This is in fact what empirical investigation reveals in the case of prototypical Western societies, including Republican Rome and Western European societies since approximately the 12th century (MacDonald 1983; 1990). Socially imposed monogamy in stratified societies is the result of a variety of internal political processes whose outcome is underdetermined by evolutionary/ecological theory or human nature/nurture. The outcome of these internal political processes is that fitness differences within the society are significantly leveled and the group is therefore an important level of adaptation in conceptualizing historical Western societies. Notice that such a result is compatible with continued fitness differences within Western societies depending on con-