

Reintroducing group selection to the human behavioral sciences

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Abstract: In both biology and the human sciences, social groups are sometimes treated as adaptive units whose organization cannot be reduced to individual interactions. This group-level view is opposed by a more individualistic one that treats social organization as a byproduct of self-interest. According to biologists, group-level adaptations can evolve only by a process of natural selection at the group level. Most biologists rejected group selection as an important evolutionary force during the 1960s and 1970s but a positive literature began to grow during the 1970s and is rapidly expanding today. We review this recent literature and its implications for human evolutionary biology. We show that the rejection of group selection was based on a misplaced emphasis on genes as "replicators" which is in fact irrelevant to the question of whether groups can be like individuals in their functional organization. The fundamental question is whether social groups and other higher-level entities can be "vehicles" of selection. When this elementary fact is recognized, group selection emerges as an important force in nature and what seem to be competing theories, such as kin selection and reciprocity, reappear as special cases of group selection. The result is a unified theory of natural selection that operates on a nested hierarchy of units.

The vehicle-based theory makes it clear that group selection is an important force to consider in human evolution. Humans can facultatively span the full range from self-interested individuals to "organs" of group-level "organisms." Human behavior not only reflects the balance between levels of selection but it can also alter the balance through the construction of social structures that have the effect of reducing fitness differences within groups, concentrating natural selection (and functional organization) at the group level. These social structures and the cognitive abilities that produce them allow group selection to be important even among large groups of unrelated individuals.

Keywords: altruism; group selection; human evolution; levels of selection; sociobiology

The existence of egoistic forces in animal life has long been recognized. It is not so well known that the idea of group-centered forces in animal life also has a respectable history. (Allee 1943, p. 519)

It is a crude oversimplification to conceive of social motives as being capable of direct derivation from a hedonic algebra of self-interest – real or fictitious – based on a few universal human drives, whatever the choice of the drives may be. (Tajfel 1981, p. 36)

These quotations illustrate a perspective in which social groups have a primacy that cannot be reduced to individual interactions. This group-level perspective can be found in biology and all branches of the human behavioral sciences (e.g., anthropology, economics, psychology, sociology). It is opposed by another perspective that treats individuals as primary and social groups as mere consequences of individual interactions. Although the conflict

between the two perspectives is often dismissed as semantic, it refuses to go away, suggesting that substantive issues are involved.

In biology, the conflict between the two perspectives has had a remarkable history. Prior to 1960, it was quite acceptable to think of social groups and even whole ecosystems as highly adapted units, similar to individuals in the harmony and coordination of their parts.¹ Williams (1966) and others argued that group-level adaptations require a process of natural selection at the group level and that this process, though theoretically possible, is unlikely to be important in nature. Their verdict quickly became the majority view and was celebrated as a major scientific advance, similar to the rejection of Lamarckianism. A generation of graduate students learned about group selection as an example of how not to think and it became almost mandatory for the authors of journal articles to assure their readers that group selection was not being invoked. Nevertheless, a positive literature began to grow in the '70s and is rapidly expanding today (Table 1).² It is no longer heretical for biologists to think of

Table 1. A guide to the biological literature on group selection since 1970. T = theoretical models (both mathematical and verbal), E = possible empirical examples (including examples not verified by experiments), F = field experiments, L = laboratory experiments, R = literature reviews, P = philosophical treatments, C = criticisms of group selection interpretations, and H = papers that are especially relevant from the standpoint of human evolutionary biology. (Theoretical; Empirical; Field; Laboratories; Reviews; Philosophical; Critiques; Human).

CITATION	T	E	F	L	R	P	C	H
Alexander and Borgia 1978	x				x	x		
Aoki 1982	x							
Aoki 1983	x							
Aviles 1986		x	x					
Aviles 1993		x	x					
Bell 1978	x							
Boehm 1981	x	x			x		x	
Boorman and Levitt 1973	x							
Boorman and Levitt 1980	x							
Boyd and Richerson 1980	x							
Boyd and Richerson 1982	x					x		
Boyd and Richerson 1985	x					x		
Boyd and Richerson 1988	x					x		
Boyd and Richerson 1989	x					x		
Boyd and Richerson 1990a	x					x		
Boyd and Richerson 1990b	x					x		
Brandon 1990					x			
Breden and Wade 1989	x	x						
Buss 1987	x	x						
Camazine and Sneyd 1991	x							
Campbell 1979	x				x	x		
Campbell 1983	x				x	x		
Campbell 1991	x				x	x		
Campbell 1993	x				x	x		
Cassidy 1978					x			
Cavalli-Sforza and Feldman 1978	x							
Chao and Levin 1981			x					
Charlesworth 1979	x							
Charlesworth and Toro 1982	x				x			
Chepko-Sade, Dow, and Cheverud 1988		x				x		
Cohen and Eshel 1976	x							
Colwell 1981	x							
Craig 1982			x					
Crespi and Taylor 1990	x		x					
Crow and Aoki 1982	x							
Crow and Aoki 1984	x							
Crozier 1987	x			x				

(continued)

Table 1. (Continued)

CITATION	T	E	F	L	R	P	C	H
Crozier and Consul 1976	x							
Damuth 1985	x							
Damuth and Heisler 1988	x					x	x	
Dugatkin 1990	x	x						
Dugatkin and Reeve 1994	x					x		
Dugatkin et al 1992	x							
Eberhard 1990	x	x						
Eibl-Eibesfeldt 1982								x
Eshel 1972	x							
Eshel 1977	x							
Eshel and Montro 1988	x							
Ewald 1993	x	x	x	x	x	x		x
Fagan 1980	x							
Findlay 1992	x							x
Fix 1985	x							x
Frank, S. A. 1986a	x							
Frank, S. A. 1986b	x							
Frank, S. A. 1987	x	x						
Gadgil 1975	x							
Garcia and Toro 1990						x		
Gilinsky and Mayo 1987							x	
Gilpin 1975	x							
Gilpin and Taylor 1988	x						x	x
Goodnight 1985						x		
Goodnight 1990a						x		
Goodnight 1990b						x		
Goodnight 1991						x		
Goodnight, Schwartz, and Stevens 1992	x							
Goodnight, K. 1992	x							
Gould 1980	x							
Govindaraju 1988		x			x			
Grafen 1984	x							x
Griesmer and Wade 1988							x	
Griffing 1977	x							
Harpending and Rogers 1987	x							x
Hausfater and Breden 1990	x	x			x			
Heisler and Damuth 1987	x							
Hull 1980							x	
Hull 1981							x	
Hull 1988							x	x
Hurst 1991	x							
Jimenez, and Casadesus 1989	x	x						
Johnson and Brown 1990					x			
Kelly 1992a	x							

(continued)

Table 1. (Continued)

CITATION	T	E	F	L	R	P	C	H
Kelly 1992b	x							
King 1990	x	x	x		x			
Kitcher, Sterelny, and Waters 1990					x			
Knaust 1991		x		x		x		
Leigh 1977	x							
Leigh 1991	x	x			x			
Levin and Kilmer 1974	x							
Lewontin 1970	x	x						
Lloyd 1988					x			
MacDonald in prep	x			x		x		
Margolis 1982	x						x	
Matessi and Jayakar 1976	x							
Matessi, Karlin, and Morris 1987	x							
Maynard Smith 1976	x			x	x			
Maynard Smith 1982b	x			x	x			
Maynard Smith 1987a	x			x	x			
Maynard Smith 1987b	x			x	x			
Mayr 1990					x			
McCauley 1989		x						
McCauley and Wade 1980			x					
McCauley and Wade 1988	x							
McCauley et al 1988		x						
Mesterton-Gibbons and Dugatkin 1992	x	x		x				
Michod 1982	x							
Michod and Sanderson 1985	x							
Mitchell 1987					x			
Mitchell 1994					x	x		
Montro and Eshel 1988	x							
Myerson, Pollock, and Swinkels 1991	x							
Nunney 1985a	x					x		
Nunney 1985b	x					x		
Nunney 1989	x							
Owen 1986	x							
Peck 1990	x						x	
Peck 1992	x							
Peck 1993	x							
Pollock 1983	x							
Pollock 1988	x							
Pollock 1989	x						x	
Pollock 1991	x						x	
Pollock in press	x						x	
Price 1970	x							
Price 1972	x							
Proctor 1989		x						

(continued)

Table 1. (Continued)

CITATION	T	E	F	L	R	P	C	H
Queller 1991	x							
Queller 1992	x							
Ratnicks 1988	x	x						
Ratnicks and Visscher 1989				x				
Reed 1978							x	
Richards 1987	x					x		x
Richardson 1983						x		
Rissing et al 1989			x	x				
Rogers 1990	x							x
Rosenberg 1983							x	
Rosenberg 1985							x	
Rushton 1989	x	x		x			x	
Seeley 1989			x	x				
Seger 1989					x			
Shanahan 1990	x	x						
Slatkin 1981	x			x				
Slatkin and Wade 1978	x							
Slatkin and Wilson 1979	x							
Smith, D. C. 1990			x					
Smith R. J. F. 1986	x							
Sober 1994						x		x
Sober 1981							x	
Sober 1984							x	
Sober 1987	x					x		
Sober 1990							x	
Sober 1992a	x					x		
Sober 1992b							x	
Sober 1993a							x	
Sober and Lewontin 1982	x						x	
Stanley 1975	x	x						
Stanley 1979	x	x						
Sterelny and Kitcher 1988							x	x
Tanaka 1991	x							
Toro and Silio 1986	x							
Treisman 1983	x					x		x
Uyenoyama and Feldman 1980a	x							
Uyenoyama and Feldman 1980b	x							
Von Schilcher and Tennant 1984							x	x
Voorzanger 1984						x		x
Vrba 1989	x					x		
Wade 1976					x			
Wade 1977					x			
Wade 1978	x				x			

(continued)

Table 1. (Continued)

CITATION	T	E	F	L	R	P	C	H
Wade 1979				x				
Wade 1982a	x							
Wade 1982b				x				
Wade 1985	x							
Wade 1991				x				
Wade and Breden 1980	x							
Wade and McCauley 1980				x				
Wade, Breden, and McCauley 1988		x						
Walton 1991						x		
Waters 1991						x		
Werren and Beukeboom 1992			x					
Werren and Beukeboom 1993	x							
Whitlock and McCauley 1990	x							
Williams 1992	x				x	x		
Williams, G. C. (ed) 1971	x			x	x			
Wills 1991		x		x				
Wilson 1976	x							
Wilson 1977a	x							
Wilson 1977b	x	x						
Wilson 1978	x							
Wilson 1980	x	x			x			
Wilson 1983a	x	x						
Wilson 1983b	x							
Wilson 1985				x				
Wilson 1987	x							
Wilson 1989	x			x		x		
Wilson 1990	x	x						
Wilson 1992a	x							
Wilson 1992b					x	x		
Wilson 1993	x				x			
Wilson and Colwell 1981	x	x						
Wilson and Dugatkin 1992	x							
Wilson and Knollenberg 1987	x		x	x				
Wilson and Sober 1989	x	x			x			
Wilson 1975	x							
Wilson, E. O. 1973	x							
Wilson, J. B. 1987	x							
Wilson, Pollack, and Dugatkin 1992	x							
Wimsatt 1980					x			
Wright 1980	x							
Wynne Edwards, V. C. 1986	x	x			x			
Zeigler 1978	x							

natural selection as a hierarchical process that often operates at the group level.

The most recent developments in biology have not yet reached the human behavioral sciences, which still know group selection primarily as the bogeyman of the '60s and '70s. The purpose of this target article is to reintroduce group selection to the human behavioral sciences. We think group selection can provide a firm foundation for a group-level perspective in the human sciences, as it has in biology. Before beginning, however, it is important to note a complication. Evolutionary approaches to human behavior have become increasingly common, as readers of *Behavioral and Brain Sciences* well know. Unfortunately, some of the most prominent evolutionary biologists interested in human behavior have themselves failed to incorporate the recent literature and still present group selection as a bogeyman (e.g., Alexander 1979; 1987; Daly & Wilson 1988; Trivers 1985; but see Table 1 entries marked "H" for exceptions). We must accordingly reintroduce group selection to human sociobiology as well as to the more traditional branches of the human sciences.

1. A brief review of the group selection controversy

1.1. The adaptationist program

In an influential paper, Gould and Lewontin (1979) criticized evolutionists for using adaptation as their only explanatory principle, to the exclusion of other factors such as genetic drift and genetic/developmental constraints. They coined the term "adaptationist program" as a pejorative and their conclusion that it cannot be the *only* tool in the evolutionist's tool kit is well taken. At the same time, their message should not obscure the fact that the adaptationist program, or "natural selection thinking" (Charnov 1982), is an extremely powerful tool for predicting the properties of organisms.

One of the virtues of the adaptationist program is that it can be used with minimal knowledge of the physiological, biochemical, and genetic processes that make up the organisms under examination. For example, imagine studying the evolutionary effects of predation on snails, seeds, and beetles. Suppose you discover that for all three groups, species exposed to heavy predation have harder and thicker exteriors than species not so exposed. The property "hard exterior" can be predicted from knowledge of the selection pressures operating on the populations. Since the exteriors of snails, beetles, and seeds are made of completely different materials, there is a sense in which these materials are irrelevant to the prediction (Campbell 1974; D. S. Wilson 1988). That is why Darwin was able to achieve his fundamental insights despite almost total ignorance of the mechanistic processes that make up organisms. Adaptationist explanations have the power to unify phenomena that are physiologically, biochemically, and genetically quite different.

The adaptationist program is valuable even if its predictions turn out to be untrue. If we know the traits that organisms will have if natural selection is the only influence on evolutionary trajectories, then deviations from these traits constitute evidence that factors other than natural selection have played a significant role. To dis-

cover whether adaptationism is true or false, optimality models are indispensable (Orzack & Sober 1994; Sober 1993b).

Although the following discussion is, in effect, a view about how the adaptationist program should be pursued, it involves no substantive commitment to the success of that program. Regardless of the scope and limits of adaptationism, the question, What would organisms be like if they were well adapted? is of paramount importance in evolutionary biology.

1.2. The adaptationist program and the biological hierarchy

The question, What would organisms be like if they were well adapted? is more complicated than it sounds. To see this, consider an imaginary population of rabbits inhabiting an island. A mutant arises that grazes more efficiently – so efficiently that a population of such mutants will overexploit their resources and become extinct. The mutation is adaptive in the limited sense of causing its bearer to have more offspring than other rabbits, but maladaptive in the larger sense of driving the population to extinction.

This example should sound familiar to human behavioral scientists because it resembles the social dilemmas that abound in human life. It corresponds to the tragedy of the commons popularized by Hardin (1968), the voting problem of economics (Margolis 1982), and the prisoner's dilemma of game theory (Rapoport & Chammah 1965). For humans and nonhumans alike, individual striving can lead to social chaos. [See also Maynard Smith: "Game Theory and the Evolution of Behaviour" *BBS* 7 (1) 1984; Caporael et al.: "Selfishness Examined" *BBS* 12 (4) 1989.]

As was previously mentioned, many biologists before the '60s uncritically assumed that natural selection evolves adaptations at upper levels of the biological hierarchy. In our imaginary example they would assume that the population of rabbits evolves to manage its resources. The possibility that adaptation at one level of the hierarchy can be maladaptive at another level was either ignored or assumed to be resolved in favor of the higher level. These sentiments, which today are called "naive group selectionism," permeated the textbooks and were espoused by many eminent biologists, including Alfred Emerson (1960), who believed that all of nature was as functionally integrated as a termite colony. As a young postdoctoral associate at the University of Chicago, G. C. Williams attended a lecture by Emerson and left muttering, "Something must be done. . ." The result was a modern classic, *Adaptation and natural selection* (Williams 1966).³

Williams's argument against higher-level adaptations came in three parts. First, he claimed that *adaptation at any level of the biological hierarchy requires a process of natural selection operating at that level*. Returning to our population of rabbits, it is easy to see that efficient grazers will evolve because they have more offspring than inefficient grazers. The negative consequences at the population level are irrelevant. However, if we imagine an archipelago in which only some of the islands contain the mutant strain, then populations driven extinct by the mutant can be replaced by other populations without

the mutant. The population-level adaptation can now persist, but only because we have added a process of natural selection at that level; fit populations replace unfit populations in the same sense that fit rabbits replace unfit rabbits within populations. This is what evolutionary biologists term group selection.

Second, Williams (1966) argued that group selection is unimportant in nature despite the fact that it is theoretically possible:

It is universally conceded by those who have seriously concerned themselves with this problem that such group-related adaptations must be attributed to the natural selection of alternative *groups* of individuals and that the natural selection of alternative alleles within populations will be opposed to this development. I am in entire agreement with the reasoning behind this conclusion. Only by a theory of between-group selection could we achieve a scientific explanation of group-related adaptations. However, I would question one of the premises on which the reasoning is based. Chapters 5 to 8 will be primarily a defence of the thesis that group-related adaptations do not, in fact exist. (p. 92)

Part of Williams's skepticism can be illustrated with our rabbit example. If migration occurs between islands, what is to prevent the mutant from "infecting" the other islands before the original population becomes extinct? Or perhaps the mutant population doesn't become extinct but merely hobbles along in a malnourished state, in which case the occasional migrant from other islands would be unable to survive. At least for this example, it seems that the parameters of the model must be very finely tuned for group-level selection to prevail against individual-level selection.

Third, Williams developed a concept of the gene as the "fundamental unit of selection" that has become a major theme in evolutionary biology, especially as amplified and extended by Dawkins (1976; 1982a). Williams claimed that groups and even individuals cannot be units of selection because they are ephemeral and do not replicate with sufficient fidelity. Every sexually reproducing organism is a unique combination of thousands of genes that will never exist again, no matter how successful reproductively. At the individual level, only clonal organisms replicate with sufficient fidelity to qualify as units of selection. For sexually reproducing organisms, the gene is the unit that is transmitted through time with high fidelity and is therefore the fundamental unit of selection (the *replicator*, in Dawkins's terminology). This is frequently used as an argument against group selection. For example, Alexander (1979) states:

In 1966 Williams published a book criticizing what he called "some current evolutionary thought" and chastised biologists for invoking selection uncritically at whatever level seemed convenient. Williams' book was the first truly general argument that selection is hardly ever effective on anything but the heritable genetic units of "genetic replicators" (Dawkins 1978) contained in the genotypes of individuals. (p. 36)

Individuals and groups appear in Williams's scheme, not as units of selection, but as *environments of the genes*. As the simplest example, consider two alleles (*A, a*) at a single diploid locus in a randomly mating population, yielding the familiar three genotypes (*AA, Aa, aa*) in Hardy-Weinberg proportions. Suppose the fitnesses of the three genotypes are $W_{AA} = 1$, $W_{Aa} = 0.75$ and $W_{aa} =$

0.5. From the gene's-eye view, the A-allele can be said to inhabit two "genotypic environments," AA and Aa, and its average fitness can be easily calculated:

$$W_A = pW_{AA} + (1 - p)W_{Aa} \quad (1)$$

The term p , in addition to being the frequency of the A-allele in the population, is also the proportion of A-alleles that exist in the AA "environment" in a randomly mating population. The fitness of the a -allele can similarly be averaged across its two genotypic environments (Aa, aa) to yield:

$$W_a = pW_{Aa} + (1 - p)W_{aa} \quad (2)$$

The A-allele will evolve whenever $W_A > W_a$, which is always the case when $W_{AA} > W_{Aa} > W_{aa}$. Note that A and a have the same fitness within the one genotypic environment that they inhabit together (the heterozygote). It is only by averaging across genotypic environments that differences in the fitness of A and a occur. Biologically informed readers will recognize W_A and W_a as the "average effects" of the two alleles used to calculate breeding values and narrow-sense heritability at the individual level (e.g., Falconer 1981; Wilson & Sober 1989).

More complicated examples can be constructed in which the population is divided into social groups that differ in allele frequencies and genotypic fitnesses. In these cases the genes inhabit a more complicated array of environments, but in principle it is always possible to calculate gene-level fitness by averaging across genotypic and social contexts. In addition, it will always be the case that A replaces a when $W_A > W_a$. This is why Williams (1986; 1992) refers to genes as "bookkeeping" devices that automatically record the net effect of multiple selection pressures.

Williams's case against group selection was strengthened by two other theories in evolutionary biology that were developed during the '60s and '70s. The first was inclusive fitness theory (also called kin selection; Hamilton 1964; Maynard Smith 1964), which explained how altruism could evolve among genetic relatives. The second was evolutionary game theory (Axelrod & Hamilton 1981; Maynard Smith 1982a; Trivers 1971; Williams 1966), which explained how cooperation could evolve among nonrelatives. These theories seemed to account for many of the phenomena that group selection had been invoked to explain. With the problems raised by Williams and two robust alternatives, the theory of group selection, never well articulated to begin with, collapsed.

Not all evolutionary biologists are familiar with the details of Williams's arguments against group selection, but the bottom line conclusion has been adopted with such conviction that we will call it Williams's first commandment: *Thou shalt not apply the adaptationist program above the level of the individual*. All adaptations must be explained in terms of the relative fitness of individuals within populations. Individual-level adaptations may have positive or negative effects at the group level, but in both cases the group-level effects are irrelevant to evolutionary change. Williams's first commandment was repeated like a mantra throughout the '60s and '70s, as every evolutionary biologist knows. Unfortunately, the mantra still echoes through the numerous accounts of evolutionary theory that are written for the human sciences and popular audiences today (e.g., Alexander 1987; Archer 1991; Cronin 1991; Daly & Wilson

1988; R. H. Frank 1988; Krebs 1987; MacDonald 1988b; Noonan 1987; Sagan & Druyan 1992).

1.3. Examining the edifice

Although Williams's and Dawkins's gene-centered view has enjoyed enormous popularity, it has one flaw that should be obvious, at least in retrospect. Naive group selectionists thought that upper levels of the biological hierarchy were like *individual organisms* in the coordination and harmony of their parts. According to Williams and Dawkins, however, even sexually reproducing organisms do not qualify as units of selection because they, like groups, are too ephemeral. If a creature such as a bird or a butterfly is not a unit of selection, then what endows it with the internal harmony implied by the word "organism"?

To answer this question, an entirely different concept needed to be invoked which Dawkins (1976) called "vehicles of selection" ("interactors" in Hull's 1980 terminology). Using one of Dawkins's own metaphors, we can say that genes in an individual are like members of a rowing crew competing with other crews in a race. The only way to win the race is to cooperate fully with the other crew members. Similarly, genes are "trapped" in the same individual with other genes and can usually replicate only by causing the entire collective to survive and reproduce. It is this property of shared fate that causes "selfish genes" to coalesce into individual organisms.¹

So far, so good, but if individuals can be vehicles of selection, what about groups? After all, we are interested in comparing groups with individuals, not with genes. Yet gene-centered theorists have scarcely addressed this question.⁴ The situation is so extraordinary that historians of science should study it in detail: a giant edifice is built on the foundation of genes as replicators, and therefore as the "fundamental" unit of selection, which seems to obliterate the concept of groups as organisms. In truth, however, the replicator concept cannot even account for the organismic properties of individuals. Almost as an afterthought, the vehicle concept is tacked onto the edifice to reflect the harmonious organization of individuals, but it is not extended to the level of groups. The entire edifice therefore fails to address the question that it originally seemed to answer so conclusively, and that made it seem so important.

This is such a crucial and unappreciated point that we want to reinforce it by quoting from *The ant and the peacock* (Cronin 1991), one of the most recent book-length treatments of evolution for a popular audience.⁵ It was chosen as one of the year's best by the New York Times and has been cited with approval by authorities such as Williams (1993), Maynard Smith (1992), and Dennett (1992).⁶ There is every reason for the reader to think that it represents state-of-the-art evolutionary biology.

Cronin (1991) agrees with us that naive group selectionists compared groups to *individuals*:

Many an ecologist, equipped with no more than a flimsy analogy, marched cheerfully from the familiar Darwinian territory of individual organisms into a world of populations and groups. Populations were treated as individuals that just happened to be a notch or two up in the hierarchy of life. (p. 278)

Her treatment of Williams is also close to our own: "Williams retaliated with two types of argument. He spelled out why genes are suitable candidates for units of selection whereas organisms, groups and so on are not . . ." (Cronin 1991, p. 286). Here Cronin commits (along with Williams) the fallacy that we outlined above. If individuals and groups are not replicators, then the replicator concept cannot be used to argue that they are different from each other! Faced with this dilemma, Cronin (1991) dutifully invokes vehicles to explain the organismal properties of individuals, with a nod to groups:

If organisms are not replicators, what are they? The answer is that they are vehicles of replicators. . . . Groups, too, are vehicles, but far less distinct, less unified. . . . In this weak sense, then, "group selection" could occur. . . . But even if they [group-level adaptations] did arise – which as we've seen is unlikely – they would in no way undermine the status of genes as the only units of replicator selection. This does not mean that higher level entities are unimportant in evolution. They are important, but in a different way: as vehicles. (p. 289)

But this is all that naive group selectionists ever claimed – that groups are like individuals by virtue of the adaptive coordination of their parts! Finally, Cronin (1991) concludes that group selection is unimportant even in the so-called weak sense:

But group selectionism (weak group selectionism) makes claims about adaptations, about characteristics that satisfy the fragmented purposes of all the genes in the group and, what's more, confer an advantage on that group over other groups. Group-level adaptations, then, are a very special case of emergent properties – so special that it would be rash to expect them to have played any significant role in evolution. Of course, the question of what role they have actually played is an empirical, not a conceptual issue. It is a factual matter about which adaptations happen to have arisen at levels higher than organisms, about the extent to which groups and other higher-level vehicles happen to have been roadworthy. (p. 290)

Cronin is in the unhappy position of a circus artist who stands on the backs of two horses, replicators and vehicles, as they gallop around the ring. The only way that she can perform this dazzling feat is by making the horses gallop in parallel. Thus, groups must fail not only as replicators but as vehicles. What Cronin cannot bring herself to say is that the replicator concept that forms the inspiration for her book is *totally irrelevant* to the question that is and always was at the heart of the group selection controversy – can groups be like *individuals* in the harmony and coordination of their parts? To answer this question we must restructure the entire edifice around the concept of vehicles, not replicators. That is exactly what the positive literature on group selection does.⁷

1.4. Taking vehicles seriously

The essence of the vehicle concept is *shared fate*, exemplified by the adage (and by Dawkins's rowing crew metaphor) "we're all in the same boat." Our restructured edifice must first be able to identify the vehicle(s) of selection in any particular biological or human situation.

In Figure 1, the biological hierarchy is shown as a

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-
-
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METAPOPULATION GROUP INDIVIDUAL GENE

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-
-
-

Figure 1. A nested hierarchy in which every unit is a population of lower-level units. The hierarchy is left open on both ends because genes are composed of subunits and metapopulations can exist in higher-order metapopulations. For example, a valley can be a metapopulation of villages, which in turn are metapopulations of kinship groups.

nested series of units, each of which is a population of lower-level units. An individual can be regarded as a population of genes and a group is obviously a population of individuals. A metapopulation is a population of groups. For example, a single field might contain hundreds of ant colonies. Each colony certainly deserves to be called a group and yet we must also recognize the collection of groups as an important entity. The hierarchy has been left open on both ends because genes are composed of subunits and metapopulations can exist in higher-order metapopulations, a fact that will become important later.

Vehicles of selection can be identified on a trait by trait basis by the following simple procedure: starting at the lowest level of the hierarchy,⁸ ask the question, "Do genes within a single individual differ in fitness?" If the answer is "no," then they share the same fate and are part of the same vehicle. Proceeding up the hierarchy, ask the question, "Do individuals within a single group differ in fitness?" If the answer is "no," then once again they share the same fate and we must proceed up the hierarchy until we find the level(s) at which units differ in fitness. This is the level (or levels) at which natural selection actually operates, producing the functional organization implicit in the word "organism."⁹ Everything below this level will acquire the status of organs and everything above this level will be vulnerable to social dilemmas.¹⁰

Already, we can make three fundamental points. First, focusing on vehicles makes it obvious that the concept of organism is not invariably linked to the individual level of the biological hierarchy. To the extent that genes can differ in fitness within single individuals, the genes will become the organisms and the individual will become a dysfunctional collection of genes. To the extent that indi-

viduals in the same group are in the same "boat" with respect to fitness, they will evolve into harmonious organs of group-level organization. In short, the organ-organism-population trichotomy can be frameshifted both up and down the biological hierarchy. Frameshifts in both directions have been documented and examples will be provided below.

Second, the status of organ versus organism versus population must be assigned on a trait-by-trait basis. It is possible for a single creature such as a wasp to be an organ with respect to some traits, an organism with respect to other traits, and a population of organisms with respect to still other traits. This may sound strange but it follows directly from the fact that fitness is a property of traits, not organisms (Sober 1984). For example, in the parasitic wasp *Nasonia vitripennis*, some males harbor what has been called the "ultimate" selfish gene, because it destroys all the other genes in the male to facilitate its own transmission (Werren 1991; Werren & Beukeboom 1992). In this case, the gene is the vehicle of selection, but most other genes in the same species evolve by standard Darwinian selection, in which case the individual is the vehicle of selection.

Third, fitness differences are not always concentrated at one level of the biological hierarchy. Individuals with trait A can be less fit than individuals with trait B within single groups, whereas groups of individuals with trait A are more fit than groups of individuals with trait B. In these cases we cannot assign the status of organ, organism, or population and must settle for some hybrid designation. As one example, Williams (1966) showed that, given certain assumptions, natural selection within single groups favors an even sex ratio whereas natural selection between groups favors an extreme female-biased sex ratio. He thought that the absence of female-biased sex ratios in nature provided conclusive evidence against group selection. Since then, moderately female-biased sex ratios have been discovered in literally hundreds of species; these reflect an equilibrium between opposing forces of within- and between-group selection (Charnov 1982; Colwell 1981; S. A. Frank 1986b; D. S. Wilson & Colwell 1981).¹¹ As we will show, altruism is another example of a hybrid trait that is selected against at the individual level but favored at the group level. We will now document our claim that the organ-organism-population trichotomy can be frameshifted both up and down the biological hierarchy.

1.4.1. Individuals as dysfunctional populations of genetic elements. Individuals are traditionally viewed as stable entities that (barring mutation) pass the same genes in the same proportions to their offspring that they received from their parents. However, this is not always the case. For example, a diploid individual can be regarded as a population of $N = 2$ alleles at each locus. The rules of meiosis usually dictate that each allele is equally represented in the gametes. Occasionally a mutation arises that "breaks" the rules of meiosis by appearing in more than 50% of the gametes, a phenomenon known as "meiotic drive" (Crow 1979). These same alleles often reduce the survival rate of individuals that possess them and can even be lethal in homozygous form. Let us apply our simple procedure to this example to identify the vehicle(s) of selection. Can genes within a single individual differ in

fitness? The answer is "yes" because the driving allele exists at a frequency of $p = 0.5$ in heterozygotes, and occurs in the gametes of those heterozygotes with a frequency of $p > 0.5$. Natural selection therefore operates at the gene level, favoring the driving allele. Now proceed up the hierarchy. Do individuals within a single population differ in fitness? Again, the answer is "yes" because individuals with the driving allele suffer higher mortality than individuals without the driving allele. Natural selection therefore operates against the driving allele at the individual level. Both the gene and the individual are vehicles of selection. If gene-level selection is sufficiently strong, the driving allele can evolve despite its negative effects on individuals.

Many other examples of natural selection within individuals could be cited, such as those involving chromosomal genes (Dover 1986), cytoplasmic genes (Cosmides & Tooby 1981), and competing cell lineages (Buss 1987). These examples have been received with great fanfare by gene-centered theorists as some sort of confirmation of their theory. However, they do not confirm the thesis that genes are *replicators* – all genes are replicators by definition and no documentation is needed. These examples are remarkable because they show that genes can sometimes be *vehicles*. They seem bizarre and disorienting because they violate our deeply rooted notion that *individuals* are *organisms*. They force us to realize that individuals are at least occasionally nothing more than groups of genes, subject to the same social dilemmas as our imaginary population of rabbits.

Why aren't examples of within-individual selection more common? Several authors have speculated that the rules of meiosis and other mechanisms that suppress evolution within individuals are themselves the product of natural selection acting at the individual level. Genes that profit at the expense of other genes within the same individual are metaphorically referred to as "outlaws" (Alexander & Borgia 1978) and the regulatory machinery that evolves to suppress them is referred to as a "parliament" of genes (Leigh 1977). Ironically, most of the authors who use these metaphors are reluctant to think of real parliaments as regulatory machines that reduce fitness differences within groups, thereby concentrating adaptation at the group level. Gene-centered theorists frameshift downward with enthusiasm but they are much more reluctant to frameshift upward.

1.4.2. Groups as organisms. Social insect colonies have been regarded as "superorganisms" for centuries. Sterile castes with division of labor, colony-level thermoregulation, and patterns of information processing that transcend single brains, all suggest intuitively that colonies are functionally organized units, built out of individual insects. This interpretation was rejected by gene-centered theorists, however, who claimed to explain the social insects without invoking group selection. Their scorn for the earlier view is illustrated by West-Eberhard (1981, p. 12; parenthetical comments are hers): "Despite the logical force of arguments against group (or colony) selection (e.g., Williams 1966), and the invention of tidy explanations for collaboration in individual terms, the supraorganism (colony-level selection) still haunts evolutionary discussions of insect sociality."

Let us apply our simple procedure to locate the vehi-

cle(s) of selection in the social insects. Can genes differ in fitness within individuals? Yes – the social insects resemble other species in this regard – but the products of selection at this level are unlikely to enhance colony function. Can individuals differ in fitness within single colonies? Yes; as one example, honey bee queens usually mate with more than one male, leading to multiple patrilines among the workers. Many insects can detect genetic similarity using odor cues and it is plausible to expect workers tending future queens to favor members of their own patriline. As with evolution within individuals, however, this kind of palace intrigue is more likely to disrupt colony function than to enhance it (Ratnieks 1988; Ratnieks & Visscher 1989). We must therefore proceed up the hierarchy and ask, “Can groups (= colonies) differ in fitness within a metapopulation?”

Unlike our archipelago of rabbits, in which the metapopulation seemed somewhat contrived, the social insects obviously exist as a population of colonies. Consider a mutation that is expressed in honeybee workers and increases the efficiency of the hive, ultimately causing the queen to produce more reproductive offspring. It is obvious that this mutation will spread, not by increasing in frequency within the hive, but by causing hives possessing the mutation to out-produce other hives. Thus, for the majority of traits that improve colony function, the colony is the vehicle of selection and can legitimately be called an organism. Focusing on vehicles, not replicators, as the central concept makes West-Eberhard's statement sound absurd. Notice also that Williams's first argument, that group-level adaptations require a process of natural selection at the group level, is correct. But his empirical claim that group selection is weak and that group-level adaptations do not exist is just plain wrong in the case of the eusocial insects – both the process and the product are manifest. The focus on genes as the “fundamental” unit of replication merely distracts from the more relevant framework based on vehicles. Fortunately, most social insect biologists now realize this and once again regard social insect colonies as “group-level vehicles of gene survival” (Seeley 1989), at least to the degree that they evolve by between-colony selection.

Before ending our discussion of the social insects it is worth asking a question that we will pose later for humans: what does it mean for a creature such as an ant or a honeybee, itself an organism in some respects, also to be part of a group-level organism? A partial answer is provided by Seeley (1989), whose elegant experiments reveal the mechanisms of colony-level adaptation. A honeybee hive monitors its floral resources over several square miles and maximizes its energy intake with impressive accuracy. If the quality of a food patch is experimentally lowered, the hive responds within minutes by shifting workers away from that patch and toward ones that are more profitable. Yet individual bees visit only one patch and have no frame of comparison. Instead, individuals contribute one link to a chain of events that allows the comparison to be made at the hive level. Bees returning from the low quality patch dance less and are themselves less likely to revisit it. With fewer bees returning from the poor resource, bees from better patches are able to unload their nectar faster, which they use as a cue to dance more. Newly recruited bees are therefore directed to the best patches. Adaptive foraging is accomplished by a decen-

tralized process in which individuals are more like neurons than decision-making agents in their own right (Camazine & Sneyd 1991; see Camazine 1991; Deneubourg & Goss 1989; Franks 1989; E. O. Wilson & Holldobler 1988, for other examples of group-level cognition in social insects). The image of a group-level mind composed of relatively mindless individuals is aptly described in D. Hofstadter's (1979) essay “Ant Fugue.” We suggest that some aspects of human mentality can also be understood as a form of group-level cognition (see below).

1.5. Finding the vehicles in Inclusive fitness theory

How was it possible for West-Eberhard and others to think that the social insects could be explained without invoking group selection? Her “tidy” alternative explanation was inclusive fitness theory, which she and almost everyone else regarded as a robust alternative to group selection. However, inclusive fitness theory is a gene-centered framework that does not identify the vehicle(s) of selection. When we rebuild inclusive fitness theory on the foundation of vehicles we discover that it is not an alternative to the idea of group selection at all (Michod 1982; Queller 1991; 1992a; Uyenoyama & Feldman 1980b; Wade 1985; D. S. Wilson 1977a; 1980). It would be hard to imagine a more important discovery, yet human behavioral scientists are almost totally unaware of it, in part because their evolutionary informants so assiduously ignore it. Even the most recent accounts of evolution for the human sciences treat inclusive fitness and group selection as separate mechanisms (e.g., Alexander 1987; 1989; 1992; Archer 1991; Daly & Wilson 1988; R. H. Frank 1988; Krebs 1987; MacDonald 1988b; Noonan 1987). We will consider one of these treatments in detail because it allows us to make a number of important points throughout the rest of our paper. Here is R. H. Frank's (1988) depiction of group selection:

Group-selection models are the favored turf of biologists and others who feel that people are genuinely altruistic. Many biologists are skeptical of these models, which reject the central Darwinian assumption that selection occurs at the individual level. In his recent text, for example, Trivers includes a chapter entitled “The group selection fallacy.” With thinly veiled contempt, he defines group selection as “the differential reproduction of groups, often imagined to favor traits that are individually disadvantageous but evolve because they benefit the larger group.” Group selectionists have attempted to show that genuine altruism, as conventionally defined, is just such a trait. . . .

Could altruism have evolved via group selection? For this to have happened, altruistic groups would have had to prosper at the expense of less altruistic groups in the competition for scarce resources. This requirement, by itself, is not problematic. After all, altruism is efficient at the group level (recall that pairs of cooperators in the prisoner's dilemma do better than pairs of defectors), and we can imagine ways that altruistic groups might avoid being taken advantage of by less altruistic groups. . . .

But even if we suppose that the superior performance of the altruistic group enables it to triumph over all other groups, the group selection story still faces a formidable hurdle. The conventional definition again, is that nonaltruistic behavior is advantageous *to the individual*. Even in an altruistic group, not every individual will be equally altruistic. When individuals differ, there will be selection pressure in favor of the least altruistic members. And as long as these individuals get

higher payoffs, they will comprise an ever-larger share of the altruistic group.

So even in the event that a purely altruistic group triumphs over all other groups, the logic of selection at the individual level appears to spell ultimate doom for genuinely altruistic behavior. It can triumph only when the extinction rate of groups is comparable to the mortality rate for individuals within them. As [E. O.] Wilson stresses, this condition is rarely if ever met in practice. (Frank 1988, pp. 37–39)

Frank's account of group selection is accurate and similar to our own rabbit example. He also accurately depicts the climate of the group selection debate during the '60s and '70s. Now here is Frank's (1988) description of inclusive fitness theory:

Biologists have made numerous attempts to explain behavior that, on its face, appears self-sacrificing. Many of these make use of William Hamilton's notion of kin selection. According to Hamilton, an individual will often be able to promote its own genetic future by making sacrifices on behalf of others who carry copies of its genes. . . .

The kin-selection model fits comfortably within the Darwinian framework, and has clearly established predictive power. . . .

Sacrifices made on behalf of kin are an example of what E. O. Wilson calls 'hard core' altruism, a set of responses relatively unaffected by social reward or punishment beyond childhood." Viewed from one perspective, the behavior accounted for by the kin-selection model is not really self-sacrificing behavior at all. When an individual helps a relative, it is merely helping that part of itself that is embodied in the relative's genes. (pp. 25–27)

Frank's exposition certainly suggests that group selection and kin selection are alternative theories that invoke

separate mechanisms. Frank himself regards them as so different that he calls one non-Darwinian and the other Darwinian!¹² Now consider the model in Figure 2, which rebuilds inclusive fitness theory on the foundation of vehicles (see Michod 1982; Queller 1991; 1992a; Sober 1991; Uyenoyama & Feldman 1980b; Wade 1985; D. S. Wilson 1977a; 1980, for more formal treatments). A dominant allele (A) codes for a behavior that is expressed only among full siblings. The behavior decreases the fitness of the actor by an amount c and increases the fitness of a single recipient by an amount b . In Figure 2, adults of the three genotypes (AA, Aa, aa) combine randomly to form six types of mating pairs (AA × AA, AA × aa). Each mating pair produces sibling groups with a characteristic proportion of altruists and nonaltruists. Thus, the sibling groups derived from AA × AA matings are entirely altruistic, the groups derived from aa × aa matings are entirely nonaltruistic and so on. Since the behavior is expressed only among siblings, the progeny of each mated pair is an isolated group as far as the expression of the behavior is concerned. Thus, any model of sibling interactions invokes a metapopulation of sibgroups.

Now let us use our simple procedure to locate the vehicles of selection. Beginning at the lowest level of the hierarchy, there is no meiotic drive or other form of selection within individuals in this example. Moving up the hierarchy, do individuals within single sibgroups differ in fitness? Yes, and natural selection at this level operates against the altruists. In all sibgroups that contain both selfish (aa) and altruistic (Aa, AA) phenotypes the former are fitter – they benefit from the latter's help

Genotypes	AA	Aa	aa			
Mated Pairs	AAxAA	AAxAa	AAxaa	AaxAa	Aaxaa	aaxaa
Sibling Groups	AA AA AA AA AA AA AA AA AA AA	AA AA AA Aa AA AA AA AA AA Aa	Aa Aa Aa Aa Aa Aa Aa Aa Aa Aa Aa Aa Aa Aa Aa	AA AA AA Aa AA AA AA AA AA Aa	aa Aa aa Aa aa Aa aa Aa aa aa Aa aa aa Aa aa	aa aa aa aa aa aa aa aa aa aa aa aa aa aa aa
Freq. of Altruists	1	1	1	.75	.50	0
Fitness of Altruist	1.70	1.70	1.70	1.42	1.14	-
Fitness of Nonaltruist	-	-	-	1.83	1.55	1.00
Group Fitness	17.0	17.0	17.0	15.25	13.50	10.00

Figure 2. A vehicle-centered version of kin selection theory. The dominant A-allele codes for an altruistic behavior. The fitness of altruists (W_A) and nonaltruists (W_S) in a given group is $W_A = 1 - c + b(Np - 1)/(N - 1)$ and $W_S = 1 + bNp/(N - 1)$, where p = the frequency of altruists in the group, N = group size, c = the cost to the altruist, and b = the benefit to the recipient. Both phenotypes have a baseline fitness of 1. Each altruist can be a recipient for $(Np - 1)$ other altruists in the group (excluding themselves). Each nonaltruist can be a recipient for all Np altruists in the group. For this example $N = 10$, $c = 0.3$, and $b = 1.0$. Random mating among the three genotypes (first line) produces six types of mated pairs (second line), which in turn produce groups of siblings (third line). The third line shows only the average sibling group for each type of mated pair. Random sampling of the gametes will produce variation around the averages. Sibling groups vary in the frequency of altruists (fourth line). Altruism is selected against at the individual level because nonaltruists have the highest fitness within all mixed groups. Altruism is favored at the group level, however, because group fitness is directly proportional to the frequency of altruists in the group.

without sharing the costs. Sibling groups are similar to other groups in this respect. Continuing up the hierarchy, can sibgroups differ in fitness within the metapopulation? Yes, and it is here that we find the evolutionary force that favors altruism. Since every altruist contributes a net fitness increment of $b-c$ to the sibgroup, the fitness of the collective is directly proportional to the number of altruists in the group. Sibgroups with more altruists out-produce sibgroups with fewer altruists.

The degree of altruism that evolves depends on the balance of opposing forces at the group and individual levels. Figure 3 shows why kin groups are more favorable for the evolution of altruism than groups of unrelated individuals. In the latter case, groups of size N are drawn directly from the global population, forming a binomial distribution of local gene frequencies. In the former case, groups of size two (the parents) are drawn from the global population and groups of size N (the siblings) are drawn from their gametes. This two-step sampling procedure increases genetic variation among groups, intensifying natural selection at the group level. Put another way, altruists are segregated from nonaltruists more in kin groups than randomly composed groups. In both cases there are mixed groups, however, and evolution within mixed groups is the same regardless of whether they are composed of siblings or nonrelatives. Notice that this explanation does not invoke the concept of identity by descent, which seems to be the cornerstone of inclusive fitness theory. There is no physical difference between two altruistic genes that are identical by descent and two

altruistic genes that are not. The coefficient of relationship is nothing more than an index of above-random genetic variation among groups (e.g., Falconer 1981, Chs. 3–5; Queller 1991; 1992a).

We invite the reader to go back to R. H. Frank's account of group selection to confirm that it describes exactly the process of kin selection portrayed in Figure 2. Dr. Jekyll and Mr. Hyde are the same person. The only discrepancy between Frank's account and Figure 2 involves the concept of extinction. Sibling groups don't last for multiple generations and don't necessarily go extinct, but rather dissolve into the larger population when the individuals become adults and have their own offspring. Thus, sibling groups (and social insect colonies) differ somewhat from our population of rabbits and the groups that Frank and Trivers had in mind. But this does not disqualify sibling groups as vehicles of selection. After all, individuals are transient collections of genes that "dissolve" into the gene pool as gametes. The ephemeral nature of groups in Figure 2 makes them more similar to individuals, not less.

Frank's account of kin selection appears so different, not because it invokes a different mechanism for the evolution of altruism, but because it utilizes a different accounting procedure for calculating gene frequency change that does not compare the fitnesses of individuals within single groups. The method correctly predicts the degree of altruism that evolves but obscures the internal dynamics of the process. In fact, when the vehicle-centered approach was first published, many biologists who thought they were familiar with inclusive fitness

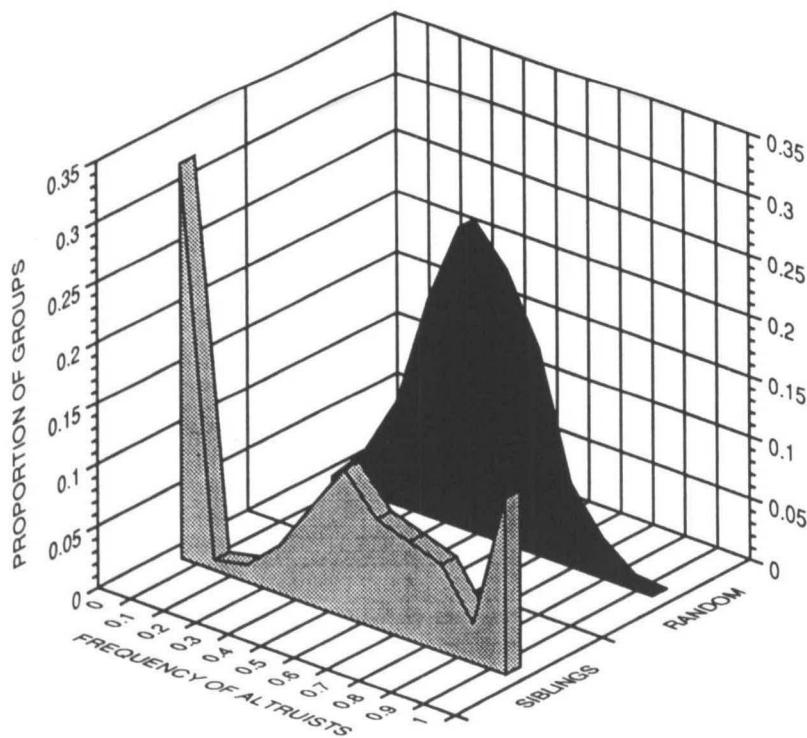


Figure 3. Variation among groups in the frequency of altruists. Altruism is coded by a dominant A allele at a frequency of $p = 0.25$ in the metapopulation, yielding a frequency of 0.438 altruists (AA and Aa) and 0.562 nonaltruists (aa). When groups of $N = 10$ are composed of unrelated individuals, the variation in the frequency of altruists between groups has a binomial distribution, as shown by the black curve. Sibling groups are created by a two-step sampling process in which groups of size $N = 2$ (the parents) are drawn from the global population and groups of size $N = 10$ (the siblings) are drawn from their gametes. This two-step sampling procedure increases genetic variation between groups, as shown by the stippled curve, intensifying natural selection at the group level. Evolution within groups always favors the nonaltruist, regardless of whether the groups are composed of siblings or unrelated individuals.

theory found it hard to believe that altruism within kin-groups is actually selected against and evolves only by a process of between-group selection.

The unification of group selection and kin selection has implications for the distinction between "genuine" and "apparent" altruism. This is an important distinction in the human behavioral sciences and evolutionary accounts such as Frank's seem to provide a tidy answer: the altruism that evolves by group selection is genuine because it entails real self-sacrifice, whereas the altruism that evolves by kin selection is only apparent because it is just genes promoting copies of themselves in other individuals. The unified theory reveals that this distinction is an artifact of the way that fitness is calculated. Any trait that is selected at the group level can be made to appear genuinely altruistic by comparing relative fitness within groups, or only apparently altruistic by averaging fitness across groups (D. S. Wilson 1992; D. S. Wilson & Dugatkin 1992). Thus, evolutionary biologists have so far contributed little but confusion to the distinction between genuine and apparent altruism.¹³

1.6. Finding the vehicles in evolutionary game theory

Evolutionary game theory (also called ESS theory for "evolutionarily stable strategy") is similar to economic game theory except that the strategies compete in Darwinian fashion, as opposed to being adopted by rational choice. It was developed to explore the evolution of cooperation and was universally considered to be an individual-level alternative to group selection. For example, Dawkins (1980) states

There is a common misconception that cooperation within a group at a given level of organization must come about through selection between groups. . . . ESS theory provides a more parsimonious alternative. (p. 360)

We will explore the relationship between game theory and group selection with a fanciful example that is based on Dawkins's rowing crew metaphor. A species of cricket has evolved the peculiar habit of scooting about the water on dead leaves in search of its resource (water lily flowers). A leaf can be propelled much better by two crickets than by one so they scoot about in pairs. Initially they were quite awkward but natural selection eventually endowed them with breathtaking morphological and behavioral adaptations for their task. Especially impressive is the coordination of the pair. They take their stations on each side of the leaf and stroke the water with their modified legs in absolute unison, almost as if they are part of a single organism. Coordination is facilitated by one member of the pair, who synchronizes the strokes by chirping at regular intervals. On closer examination it was discovered that the chirps not only coordinate movements but also steer the little craft. A low-pitched chirp causes the chirper to row harder and a high-pitched chirp causes the nonchirper to row harder. The captain (as the chirper came to be called) adjusts its pitch to correct for asymmetries in the shape of the leaf and also to change direction as lily pads hove into view. Either member of the pair can act as captain; the important thing is that there be only one.

The evolution of any particular trait in this example can be examined with a 2-person game theory model. For example, consider two types of crickets (A1 and A2) that

differ in their ability to synchronize with their partner's movement. If p is the frequency of A1 in the population and if pairing is at random, then three types of pairs exist (A1A1, A1A2, A2A2) at frequencies of p^2 , $2p(1 - p)$ and $(1 - p)^2$. Coordination, and therefore fitness, is directly proportional to the number of A1 individuals in the pair, as shown by the payoff matrix in Figure 4a. The fitness of the two types, averaged across pairs, is $W_{A1} = 5p + 4(1 - p)$ and $W_{A2} = 4p + 3(1 - p)$.

This is not a very interesting game theory model because it doesn't pose a dilemma. $W_{A1} > W_{A2}$ for all values of p , making it obvious that A1 will evolve. However, this should not obscure a more fundamental point, that the pair is the vehicle of selection. If we apply our procedure we find no fitness differences between individuals within a pair, in which case A1 can evolve only by causing pairs to succeed relative to other pairs. The fact that the pairs are ephemeral, perhaps lasting only a fraction of an individual's lifetime, is irrelevant. Persistence is a requirement for replicators, not vehicles. Coordination evolves among the individuals for exactly the same reason that it evolves among genes within individuals, because they are "in the same boat" as far as fitness differences are concerned.

More generally, evolutionary game theory deploys a metapopulation model, in which individuals exist within groups that exist within a population of groups. When this elementary fact is recognized, Dawkins's statement quoted earlier makes as little sense as West-Eberhard's statement about the social insects. Cooperation evolves by group-level selection in a game theory model as surely as cooperation among genes evolves by individual-level selection in a standard population genetics model.¹⁴ In fact, the two models are mathematically identical; we can go from one to the other merely by relabelling A1 and A2

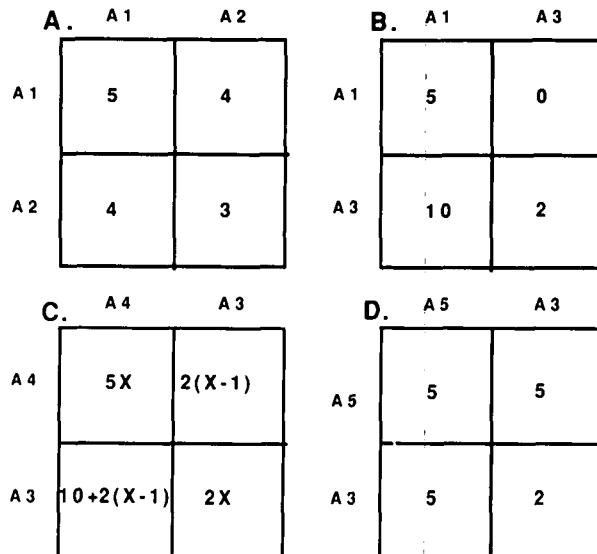


Figure 4. Four payoff matrices that represent (A) pure between-group selection, (B) a strong conflict between levels of selection, (C) a weak conflict between levels of selection (X is the average number of interactions between members of each pair), and (D) a return to pure between-group selection. Within-group selection is absent from the first example by virtue of the situation, since coordination has an equal effect on both occupants of the leaf. Within-group selection is absent from the fourth example by virtue of an adaptation, since the "outlaw" A3 type cannot operate in the presence of the "parliament" A5 type.

as "alleles" rather than as "individuals" and calling the pair a zygote (Hamilton 1971; Holt 1983; Maynard Smith 1987a; 1987b; D. S. Wilson 1983a; 1989; 1990).

Continuing our example, suppose that a mutant type (A3) arises that rushes onto the lily pad at the moment of arrival, kicking the boat away and setting its hapless partner adrift. If both members of the pair are the A3 type, however, they collide and have a probability of drowning. The pay-off matrix for this situation is shown in Figure 4b and the average fitness of the two types is $W_{A1} = p(5) + (1 - p)(0)$ and $W_{A3} = p(10) + (1 - p)(2)$.

This model is more interesting because it constitutes a social dilemma. A3 evolves despite the fact that it disrupts group-level functional organization. Applying our procedure, we find that the nasty behavior is favored by within-group selection; A3 is fitter than A1 within pairs. Cooperation, as before, is favored by between-group selection; A1A1 and A1A3 pairs are fitter than A3A3 pairs. By renaming the individuals "alleles" and the pairs "zygotes," we have the example of meiotic drive described in section 1.4.1, paragraph 1.

Continuing our example, suppose that a new mutant (A4) arises that can remember the previous behavior of its partner. It acts honorably toward new partners and thereafter imitates its partner's previous behavior. This is the famous "tit-for-tat strategy" (Axelrod & Hamilton 1981) that can evolve above a threshold frequency, given a sufficient probability of future interactions (Fig. 4c). Applying our procedure, we find that natural selection still favors A3 over A4 within pairs because A4 loses during the first interaction. A4 reduces but does not eliminate its fitness disadvantage within groups by changing its behavior and it evolves only because groups of A4A4 outperform groups of A4A3 and A3A3.¹⁵

Finally, suppose that yet another mutant arises (A5) that grabs hold of its partner with one of its free legs, preventing it from leaping prematurely onto the lily pad. The payoff matrix for A5 versus A3 is shown in Figure 4d. Applying our procedure, we find that fitness differences within groups have been eliminated while between-group selection still favors A5A5 and A5A3 over A3A3. A5 is like a dominant allele in the sense that A5A5 and A5A3 groups are phenotypically identical. Within-group selection has been eliminated by an evolved trait. Once again the pair has achieved a harmony and coordination that invites comparison with an organism, but with some safeguards built in, similar to the rules of fair meiosis at the genetic level.

How was it possible for Dawkins and virtually all other evolutionary biologists to regard game theory as an individualistic theory that does not require group selection? The answer is that groups were treated as "environments" inhabited by individuals, in exactly the same sense that Williams regarded individuals as "environments" inhabited by genes. Averaging the fitness of individual types across groups combines selection at all levels into a single measure of "individual fitness" that correctly predicts the outcome of natural selection but loses sight of the vehicles that natural selection actually acts upon. Selection can operate entirely at the group level (as it does in Figure 4a and d) and still be represented in terms of individual fitnesses simply because the average A2 (or A5) is more fit than the average A1 (or A3). This definition of what "individual selection" favors is synonymous with "any-

thing that evolves, regardless of the vehicles of selection." Of course, individuals are not replicators and we can make them disappear along with groups by averaging the fitness of genes across all contexts, arriving at a definition of "gene selection" as "anything that evolves, regardless of the vehicles of selection." These overextended definitions of individual and gene selection have misled a generation of biologists into thinking that natural selection almost never occurs at the level of groups.

In this review we have concentrated on showing how the seemingly competing theories of kin selection, evolutionary game theory, and group selection have been united into a single theory of natural selection acting on a nested hierarchy of units. The unified theory does more than redescribe the familiar results of kin selection and game theory, however; it also predicts that natural selection can operate on units that were never anticipated by kin selection and game theory, such as multigenerational groups founded by a few individuals (e.g., Aviles 1993; D. S. Wilson 1987), large groups of unrelated individuals (Boyd & Richerson 1985; 1990a; 1990b), and even multi-species communities (Goodnight 1990a; 1990b; D. S. Wilson 1976; 1980; 1987). For example, accounts of human evolution that are based on nepotism and reciprocity often conclude that prosocial behavior in modern humans is maladaptive because it is not confined to genetic relatives and is often performed without expectation of return benefits (e.g., Ruse 1986; but see Alexander 1987). Later we will argue that these prosocial behaviors can be adaptive because group-level vehicles exist that are larger than the kin groups and very small groups modelled by kin selection and evolutionary game theory.

We summarize our review of group selection in biology as follows: Williams's (1966) argument against group selection came in three parts: (a) higher-level adaptations require higher levels of selection, (b) higher levels of selection are theoretically possible but unlikely to occur in nature, (c) the gene is the fundamental unit of selection because it is a replicator. The third part of this argument is irrelevant to the question of whether groups can be like individuals in the harmony and coordination of their parts. As far as we can tell, all gene-centered theorists now concede this point (e.g., Dawkins 1982a; 1989; Grafen 1984; Williams 1992). Taking vehicles seriously requires more than acknowledging a few cases of group selection, however; it demands a restructuring of the entire edifice. It is a mistake to think there is one weak group-level theory and two strong individual-level theories to explain the evolution of altruism/cooperation. Rather, there is one theory of natural selection operating on a nested hierarchy of units, of which inclusive fitness and game theory are special cases. When we focus on vehicles of selection, the empirical claim that constitutes the second part of Williams's argument disintegrates, but the first part remains intact. Adaptation at any level of the biological hierarchy requires a process of natural selection at that level.

As might be expected from such a radical restructuring, some biologists who previously regarded group selection with contempt have found it difficult to accept this Cinderella-like reversal of fortunes. Thus, a large group of knowledgeable biologists who are perfectly comfortable with the hierarchical approach (see Table 1) coexists with another large group whose members adhere to the earlier

view. We think that the views of the former group are in the process of replacing the views of the latter. The replacement process is painfully slow, however, partly because the gene-centered view is so thoroughly entrenched and partly because the major gene-centered theorists have been reluctant to acknowledge the consequences of taking vehicles seriously. As one example, Sterelny and Kitcher (1988) manage to defend the selfish gene concept without even considering the question of whether groups can be vehicles of selection.¹⁶ We make these bold statements to provoke a response. If gene-centered theorists wish to rebut our account, let them speak in the commentary section that follows this paper. Otherwise, let the replacement process continue at a faster pace. All of the major developments that we have reviewed are over ten years old and it is time for them to be acknowledged generally.

2. Group selection and human behavior

In his description of honeybee colonies as superorganisms, Seeley (1989) wrote:

... larger and more complex vehicles have evidently proved superior to smaller and simpler vehicles in certain ecological settings. By virtue of its greater size and mobility and other traits, a multicellular organism is sometimes a better gene-survival machine than is a single eukaryotic cell. ... Likewise, the genes inside organisms sometimes fare better when they reside in an integrated society of organisms rather than in a single organism because of superior defensive, feeding, and homeostatic abilities of functionally organized groups. (p. 546)

This statement applies almost as well to humans as to honeybees. Nevertheless, group-level functional organization in humans is usually portrayed as a byproduct of individual self-interest. Even the most recent evolutionary accounts of human behavior are based on Williams's first commandment, and the triumph of "individual selection" in biology is often used to justify the individualistic perspective in the human behavioral sciences.

We think that the hierarchical theory of natural selection leads to a very different conclusion. Individualism in biology and in the human sciences both fail for the same reasons. As far as human evolution is concerned, group-level functional organization is not a "byproduct" of self-interest in humans any more than it is in honeybees. The metapopulation structure of human interactions is manifest; individuals live in social groups which themselves comprise a population of social groups. Even a relatively small social unit such as a village is a metapopulation of still smaller groups such as kinship units or coalitions of unrelated individuals. Genetic variation among human groups is not as great as among beehives, but, as we will attempt to show, human cognitive abilities provide other mechanisms for concentrating natural selection at the group level, even when the groups are composed of large numbers of unrelated individuals (see also, Alexander 1987; 1989; Boyd & Richerson 1985, 1990a; 1990b; Knauth 1991).

Individualistic accounts of human behavior do not ignore these facts (e.g., Alexander 1979; 1987; 1989; 1992), but they are able to remain individualistic only by ignoring the concept of vehicles. As soon as we make vehicles the center of our analysis, group selection emerges as an

important force in human evolution and the functional organization of human groups can be interpreted at face value – as adaptations that evolve because groups expressing the adaptations outcompeted other groups. The same adaptations can be, and often are, selectively neutral or even disadvantageous within groups. In the following sections we will sketch some of the implications of the hierarchical view for the study of human behavior.¹⁷

2.1. The new group selection is not a return to naive group selection

Some biologists have been reluctant to accept group selection in any form because they fear it will encourage the uncritical thinking of Emerson and others who simply assumed the existence of higher-level adaptations (e.g., Maynard Smith 1987a; 1987b). Behavioral scientists may share this reluctance because every branch of the human sciences seems to have thinkers like Emerson (1960) and Wynne-Edwards (1962; 1986) who treat social groups as the unit of adaptation, as if individuals and their strivings scarcely exist. We therefore want to stress, in the strongest possible terms, that these views are not supported by modern group selection theory. Consider the example within biology of the Gaia hypothesis (Lovelock 1979), which portrays the entire planet as a self-regulating organism. Even a passing knowledge of group selection theory exposes Gaia as just another pretty metaphor because planet-level adaptation would require a process of between-planet selection (Wilson & Sober 1989). Grandiose theories of human societies as organisms would be correct only if natural selection operated *entirely* at the societal level, which no one proposes. The hierarchical theory's attention to mechanism makes it easy to discredit such "theories" both in biology and the human sciences.

2.2. Groups are real

Having distanced ourselves from naive group selection, we want to stress with equal force that it is legitimate to treat social groups as organisms, to the extent that natural selection operates at the group level. Williams's first commandment (*Thou shalt not apply the adaptationist program above the individual level*) is fundamentally wrong. To see this, consider a simplified situation in which natural selection acts entirely at the individual level, in which case genes within individuals become entirely cooperative and individuals within the population frequently face conflicts of interest that lead to social dilemmas. Using the adaptationist program at the individual level leads to the celebrated insights that we discussed at the beginning of this paper. Using the adaptationist program at the population level leads to the errors of naive group selection that Williams so effectively exposed. But now suppose that someone misleadingly suggests that we should not use the adaptationist program at the individual level – that the fitness of individuals is actually irrelevant to the evolutionary process; it is only gene-level fitness that counts. This misleading advice would have us apply the adaptationist program *below* the level at which natural selection actually operates.

In a sense, this is just what adopting the gene's-eye view of Williams and Dawkins encourages us to do. Even they do not take it seriously enough to abandon the

individual's-eye view, however, since they invoke the equivalence of gene fitness and individual fitness when the latter are vehicles of selection. In practice, most biologists pay passing tribute to the gene as the "fundamental" unit of selection and think about adaptation at the individual level as they always have (e.g., Grafen 1984, quoted in note 4; Maynard Smith 1987a, p. 125). We submit that evolutionary biologists would be severely handicapped if they could not ask the simple question, What would a well adapted individual be like? Yet that is the very question that is prohibited at the group level by Williams's first commandment. If commandments are needed, we suggest the following: *Thou shalt not apply the adaptationist program either above or below the level(s) at which natural selection operates.* This statement avoids both the excesses of naive group selection and the excesses of naive individual and gene selection that we have outlined above.

According to Campbell (1993), the human behavioral sciences are dominated by something very similar to Williams's first commandment:

Methodological individualism dominates our neighboring field of economics, much of sociology, and all of psychology's excursions into organizational theory. This is the dogma that all human social group processes are to be explained by laws of individual behavior – that groups and social organizations have no ontological reality – that where used, references to organizations, etc. are but convenient summaries of individual behavior. . . . We must reject methodological individualism as an a priori assumption, make the issue an empirical one, and take the position that groups, human social organizations, might be ontologically real, with laws not derivable from individual psychology. . . . One of my favorite early papers (Campbell 1958) explicitly sides with that strident minority of sociologists who assert that "Groups are real!" even though it finds human organizations "fuzzier" than stones or white rats. (p. 1)

The hierarchical theory of natural selection provides an excellent justification for regarding groups as "real." Groups are real to the extent that they become functionally organized by natural selection at the group level. However, for traits that evolve by within-group selection, groups really should be regarded as byproducts of individual behavior. Since group selection is seldom the only force operating on a trait, the hierarchical theory explains both the reality of groups that Campbell emphasizes and the genuinely individualistic side of human nature that is also an essential part of his thinking.¹⁸

2.3. Altruism and organism

Group selection is often studied as a mechanism for the evolution of altruism. We have also seen that groups become organisms to the extent that natural selection operates at the group level. Although the concepts of altruism and organism are closely related, there is also an important difference. Altruism involves a conflict between levels of selection. Groups of altruists beat groups of nonaltruists, but nonaltruists also beat altruists within groups. As natural selection becomes concentrated at the group level, converting the group into an organism, the self-sacrificial component of altruism disappears. In other words, *an object can be an organism without its parts behaving self-sacrificially.*

The distinction between altruism and the interactions

among parts of an organism is illustrated by our fanciful cricket example. The four payoff matrices in Figure 4 represent (a) pure between-group selection, (b) strong conflict between levels of selection, (c) weak conflict between levels of selection, and (d) a return to pure between-group selection. Within-group selection is absent from the first example by virtue of the situation, since coordination has an equal effect on both occupants of the leaf. Within-group selection is absent from the fourth example by virtue of an adaptation, since the "outlaw" A3 type cannot operate in the presence of the "parliament" A5 type.

It might seem that group-level adaptations would be easiest to recognize in group-level organisms. Ironically, the opposite is true, at least from the individualistic perspective. Individualists acknowledge group-level adaptations when they are easily exploited within groups, but when they are protected, or when exploitation is not possible by virtue of the situation, group-level adaptations are seen as examples of individual self-interest, despite the fact that they evolve purely by between-group selection and result in total within-group coordination. Payoff matrices such as 4a and 4d are seldom even considered by game theorists because their outcome is so obvious. In the absence of fitness differences within groups, any amount of genetic variation between groups is sufficient to select for A1 and A5, including the variation that is caused by random pairing. It is only by adding within-group selection that we can generate the social dilemmas that are deemed interesting enough to model. A1 and A5 should not be viewed as examples of self-interest, however, just because they easily evolve! As we have seen, groups are the vehicles of selection in these examples as surely as individuals are the vehicles in standard Darwinian selection. To call A1 and A5 examples of self-interest is to place them in the same category as A3, which evolves by within-group selection and disrupts group-level organization. Putting it another way, by lumping together the products of within- and between-group selection, the individualistic perspective does not distinguish between the outlaw and the parliament, turning "self-interest" into a concept that is as empty as it is universal.

Failure to recognize group-level adaptation in the absence of altruism extends far beyond game theory. We present an example from Alexander (1987) in detail, in part because he is one of the most influential biologists writing on human evolution. Alexander envisions moral systems as levelers of reproductive opportunities within groups:

The tendency in the development of the largest human groups, although not always consistent, seems to be toward equality of opportunity for every individual to reproduce via its own offspring. Because human social groups are not enormous nuclear families, like social insect colonies . . . competition and conflicts of interest are also diverse and complex to an unparalleled degree. Hence, I believe, derives our topic of moral systems. We can ask legitimately whether or not the trend toward greater leveling of reproductive opportunities in the largest, most stable human groups indicates that such groups (nations) are the most difficult to hold together *without* the promise or reality of equality of opportunity. (p. 69)¹⁹

Alexander explicitly compares human moral systems to

the genetic rules of meiosis that eliminate fitness differences within individuals:

A corollary to reproductive opportunity leveling in humans may occur through mitosis and meiosis in sexual organisms. It has generally been overlooked that these very widely studied processes are so designed as usually to give each gene or other genetic subunit of the genome . . . the same opportunity as any other of appearing in the daughter cells. . . . It is not inappropriate to speculate that the leveling of reproductive opportunity for intragenomic components – regardless of its mechanism – is a prerequisite for the remarkable unity of genomes. (p. 69)

Since the rules of meiosis concentrate natural selection at the individual level, producing individual-level organisms, moral rules must concentrate natural selection at the group level, producing group-level organisms – right? Wrong. Here is Alexander's verdict on group selection:

Finally, many easily made observations on organisms indicate that selection is most effective below group levels. These include such things as evidence of conflicts among individuals within social groups, failure of semelparous organisms (one-time breeders) to forego reproduction when resources are scarce, and strong resistance to adopting nonrelatives by individuals evidently long evolved in social groups. None of these observations is likely if the individual's interests are consistently the same as those of the group or if, to put it differently, allelic survival typically were most affected by selection at the group level. (p. 37–8)

All of these examples involve altruistic traits that are highly vulnerable to exploitation within groups. The only evidence that Alexander will accept for group selection is extreme self-sacrifice. Somehow, Alexander manages to combine a strong emphasis on between-group competition and opportunity leveling within groups with a belief that group selection can be dismissed and that everything, parliaments and outlaws alike, is a product of self-interest.²⁰ To make matters worse, Alexander speaks for the majority of biologists interested in human behavior. For example, here is Daly and Wilson's (1988) tidy statement about human morality:

If conscience and empathy were impediments to the advancement of self-interest, then we would have evolved to be amoral sociopaths. Rather than representing the denial of self-interest, our moral sensibilities must be intelligible as means to the end of fitness in the social environment in which we evolved. (p. 254)

We hope the reader recognizes the familiar pattern of treating groups as “environments” inhabited by individuals and defining self-interest as “anything that evolves” without any consideration of vehicles. Alexander, Daly, and M. Wilson join the anti-group-selection chorus and then provide dozens of examples of human groups as vehicles of selection without ever acknowledging what gene-centered theorists have already conceded – that group selection is a “vehicle” question.

Alexander's theory of moral systems can be rebuilt on the foundation of vehicles as follows: human adaptations can evolve along two major pathways; (a) by increasing the fitness of individuals relative to others within the same social group, and (b) by increasing the fitness of social groups as collectives, relative to other social groups. Both pathways have been important in the evolution of the psychological mechanisms that govern human behavior. Sometimes group selection is important just by virtue of the situation. For example, the only way to defend a

village might be to build a stockade, which, by its nature, benefits the collective. We are not surprised to see villagers building stockades, even when they are genetically unrelated to each other. We are not surprised when they coordinate their efforts in ways that invite comparison to a single organism. Nor do we regard them as especially morally praiseworthy as they feverishly work to save their collective skins. But building the stockade is not *selfish* just because it is *reasonable*. Applying our procedure, we find that the village is the vehicle of selection. We expect the stockade to be built for the same reason that we expect A1 and A5 to evolve in the game theory models – because in this particular situation group-level selection is very strong relative to within-group selection. If we define behaviors on the basis of fitness effects (as all evolutionists do), and if we want our terminology to reflect the vehicle(s) that natural selection acts upon, we should call stockade-building *groupish*, not *selfish*.

Many other situations in human life provide opportunities for adaptation via the first pathway, by increasing the fitness of individuals relative to others within the same social group. Even with our stockade example we can imagine a temptation to cultivate selfishly one's own garden or romantic possibilities, as others build the stockade. The use of the word *selfish* is fully appropriate here because the individual is the vehicle of selection whose behaviors tend to disrupt group-level functional organization.

The balance between levels of selection is not determined exclusively by the situation, however. Adaptive human behavior not only reflects the balance between levels, it can also alter the balance between levels. Moral sentiments and moral social systems may function as “rules of meiosis” that often concentrate fitness differences, and therefore functional organization, at the group level. This is the core of Alexander's thesis. When stated in terms of vehicles, however, Alexander's theory acquires a familiar and conventional ring that is absent from his own account. Moral systems are defined as social organizations designed to maximize the benefit of the group as a collective. Immoral behaviors are defined as behaviors that benefit individuals at the expense of other individuals within the same group. These are close to the concepts of moral and immoral behavior in folk psychology.²¹ The shock value of Alexander's account, in which the gentle reader is made to face the grim reality that all is self-interest, evaporates when we realize that, for Alexander, self-interest is everything that evolves, at all levels of the biological hierarchy.²² We will return to moral systems with an empirical example, but first we must consider the important issue of psychological motivation.

2.4. Psychological selfishness and its alternatives

Dawkins portrays genes as psychologically selfish entities that manipulate their environment, including the genotypic environment in which they reside, to increase their own fitness. This image is obviously metaphorical, allowing Dawkins to use a familiar human reasoning process to describe the outcome of natural selection. The metaphor is relatively innocuous because there is no danger that it can be taken literally. No one believes that genes are intentional systems of any sort, much less systems motivated by self interest.

Frameshifting upward, it is possible to portray individuals as psychologically selfish entities that manipulate their environment, including the social environment in which they reside, to increase their own fitness. This image of "selfish individuals" may also be metaphorical, but it is more insidious because it *can* be taken literally. In other words, it is possible to believe that individuals really are intentional systems motivated entirely by self-interest and this is, in fact, the individualistic perspective that pervades the human sciences.

To distinguish mechanisms from metaphors, it is useful to think of a psychological motive as a strategy in the game-theoretic sense, which produces a set of outcomes when it interacts with itself and with other strategies. Thus, a psychologically selfish individual (however defined) will be motivated to behave in certain ways with consequences for itself and others. A psychologically altruistic individual (however defined) will be motivated to behave in other ways with a different set of payoffs. Within an evolutionary framework, the empirical claim that individuals are motivated entirely by self-interest must be supported by showing that the psychologically selfish strategy prevails in competition with all other strategies.

Psychological motives have seldom been analyzed in this way (but see Alexander 1987, R. H. Frank 1988); we suggest that this will be a productive line of inquiry in the future. We also predict that two general conclusions will emerge: first, it is extremely unlikely that any single strategy will prevail against all other strategies. Even the famous tit-for-tat strategy, which is robust in the narrow context for Axelrod's (1980a; 1980b) computer tournaments, is vulnerable to a host of other strategies in more complex and realistic environments (e.g., Boyd & Lorberbaum 1987; Dugatkin & Wilson 1991; Feldman & Thomas 1987; Peck & Feldman 1986). Thus, *any* monolithic theory of proximate motives is destined to fail, including the monolithic theory of psychological selfishness. We should expect a diversity of motives in the human repertoire that is distributed both within and among individuals.

Second, the very opposite of psychological selfishness can be highly successful, especially when natural selection operates at the group level. To see this, consider an individual who identifies so thoroughly with his group that he doesn't even consider the possibility of profiting at the expense of his fellows. This individual will be vulnerable to exploitation by members of his group who are less civic-minded. But groups of individuals who think in this way will probably be superior in competition with other groups whose members are less civic-minded. It follows that intense between-group competition will favor psychological mechanisms that blur the distinction between group and individual welfare, concentrating functional organization at the group level. Alexander (1988) himself provides a good example in a review of Richards (1987) when he describes his own military experience:

In the army in which I served one was schooled so effectively to serve the welfare of his unit (community?) that not only the contract altruism that Richards says is inferior to his "pure" altruism, but the intent that he requires, both disappear in a kind of automaticity that ceases to involve any deliberateness, either in maintenance of the contract signed when drafted or enlisted, or in explicitly serving the rest of one's unit. (p. 443)

Quibbles about the definition of altruism aside, nothing more is required to convert a social group into an organism. Critics may argue that the selfless attitude of a well-trained soldier is not adopted by individual choice but imposed by an indoctrination process and reinforced by sanctions against disloyalty that make it disadvantageous to cheat. We disagree in two ways. First, individuals are not always drafted into these groups and often rush to join them, enthusiastically embracing the doctrine, refraining from cheating and enforcing the sanctions against others. Their self-interest is not taken from them but willingly abandoned. Second, even when imposed, indoctrination and sanctions are best regarded as group-level rules of meiosis that reduce the potential for fitness differences within groups, concentrating functional organization at the group level. An entity can be an organism without the parts behaving self-sacrificially (for an evolutionary model of psychological altruism *per se*, see R. H. Frank 1988).

Since humans have lived in small groups throughout their history, it is reasonable to expect the evolution of psychological mechanisms that cause them easily to become "team players" in competition with other groups. We do not expect these to be the only motives that guide human behavior, but rather a module that is facultatively employed under appropriate conditions. In fact, there is abundant empirical evidence that humans coalesce into cooperative teams at the merest suggestion of a meta-population structure in which groups can compete against other groups (e.g., Dawes et al., 1988; Hogg & Abrams 1988; Sherif et al. 1961; Tajfel 1981). Members of the same group often share a feeling of high regard, friendship, and trust that is based not on any prior experience but merely on the fact that they are members of the same group. Exploitation within groups is often avoided even when opportunities, without any chance of detection, are experimentally provided (e.g., Caporael et al. 1989). Group formation is as spontaneous in children as it is in adults (e.g., Sherif et al. 1961). These are the earmarks of an evolved "Darwinian algorithm" (*sensu* Cosmides & Tooby 1987) that predisposes humans for life in functionally organized groups. The algorithm appears paradoxical only when we consider its vulnerability to more selfish algorithms within groups. The advantages at the group level are manifest.

It is important to stress that we have not merely converged on a view that is already well accepted within the human sciences. Proponents of alternatives to psychological selfishness are better described as an embattled minority who must constantly defend themselves against a monolithic individualistic world view (e.g., Battson 1991; Campbell 1993; Caporael et al. 1989; Mansbridge 1990; Simon 1991). As one example, most economists assume that individuals act in the interest of the company that employs them only because the company pays them enough to make it worthwhile from the standpoint of the individual's personal utility. According to Simon (1991), real people who are satisfied with their jobs do not distinguish between their own and their company's utility, but rather adopt the company's interest as their own interest. Even the lowest level employees make executive decisions that require asking the question, What is best for the company? and which go far beyond the actual requirements of the job. In fact, one of the most effective forms of protest by dissatisfied employees is

"work to rule," in which people perform their jobs to the letter and the company comes to a grinding halt. In modern life, as in ancient times, group-level function requires individuals who to a significant degree take the group's goals as their own. This is a radical proposal within economics, however, and not the majority view.

2.5. Group-level cognition

Goal-oriented behaviors are typically accomplished by a feedback process that includes the gathering and processing of information. Although the entire process can be described as intentional (e.g., the wolf *tries* to catch the deer), the elements of the process cannot (the neuron does not *try* to fire; it merely *does* fire when stimulated at enough synapses; Dennett 1981).

We are accustomed to regarding individuals as intentional systems with their own self-contained feedback processes. Group selection raises another possibility in which the feedback process is distributed among members of the group. We have already provided an example for honeybee colonies in which individuals behave more like neurons than intentional agents in their own right. Similar examples have scarcely been considered for humans and our main purpose here is to define the question, rather than to answer it.

Modern governmental and judicial systems are sometimes designed to produce adaptive outcomes at the level of the whole system but not at the level of the component individuals. Science is sometimes portrayed as a similar process that generates knowledge only at the group level (e.g., Hull 1988c; Kitcher 1993). The invisible hand metaphor in economics invokes the image of an adaptive system that organizes itself out of neuronlike components, although the metaphor is more often stated as an ideology than as a testable research program.²³

The invisible hand notwithstanding, research on decision making in small groups reveals a complex process that does not always yield adaptive solutions (Hendrick 1987a; 1987b). Groups even make decisions that would be regarded as foolish by every member of the group (Allison & Messick 1987). This research is important because it shows that intelligent individuals do not automatically combine to form intelligent groups. Adaptive decision making at the small group level may require a highly specified cognitive division of labor. Since decision making has occurred in small groups throughout human history, it is reasonable to expect "Darwinian algorithms" that cause individuals to relinquish their capacity to act as autonomous intentional agents and to adopt a more limited role in a group-level cognitive structure. The architecture of group-level cognition might simply take the form of "leaders" who act as self-contained intentional agents and "followers" who abide by the decisions of others. Alternatively, even so-called leaders may be specialists in a feedback process that is distributed throughout the group. These questions can only be asked by recognizing the group as a potentially adaptive entity.

2.6. An example of a human group-level "organism"

We conclude by providing a possible example of extreme group-level functional organization in humans and the

background conditions that make it possible. The Hutterites are a fundamentalist religious sect that originated in Europe in the sixteenth century and migrated to North America in the nineteenth century to escape conscription. The Hutterites regard themselves as the human equivalent of a bee colony. They practice community of goods (no private ownership) and also cultivate a psychological attitude of extreme selflessness. The ultimate Hutterite virtue is "Gelassenheit," a word that has no English equivalent, which includes "the grateful acceptance of whatever God gives, even suffering and death, the forsaking of all self-will, all selfishness, all concern for private property" (Ehrenpreis 1650/1978). Nepotism and reciprocity, the two principles that most evolutionists use to explain prosocial behavior in humans, are scorned by the Hutterites as immoral. Giving must be without regard to relatedness and without any expectation of return. The passion for selflessness is more than just sermonizing and frequently manifests itself in action. For example, Claus Felbinger's "Confession of Faith" (1560/1978) provides an eloquent statement that a Hutterite blacksmith gave to Bavarian authorities, after their efforts to make him recant had failed and before they executed him for his beliefs.

The extreme selflessness of the Hutterites can be explained in at least three ways. First, many authors, both inside and outside of biology, think of culture as a process that frequently causes humans to behave in ways that are biologically maladaptive. By this account, the Hutterites are influenced by (unspecified) cultural forces and their behavior cannot be explained by any biological theory, including the theory of group selection.

Second, some evolutionists have tried to explain widespread altruism in humans as a product of manipulation, in which the putative altruists are essentially duped into behaving against their own interests for the benefit of the manipulator (e.g., Dawkins 1982a; 1989). If people can be fooled into believing that a life of sacrifice will lead to a pleasant afterlife, for example, then perpetrating that belief in others becomes an example of individual self-interest. By this account, we might expect some Hutterites (such as the leaders) to profit at the expense of their duped brethren.

Third, it is possible that humans have evolved to willingly engage in selfless behavior whenever it is protected by a social organization that constitutes a group-level vehicle of selection. The relatively small group-level vehicles of kinship groups and cooperating dyads are already well recognized. The hypothesis we wish to explore asserts that the Hutterites constitute a less familiar case in which the vehicle is a relatively large group of individuals and families that are genetically unrelated to each other. If this interpretation is correct, then group selection theory should be able to predict some major features of Hutterite social organization and ideology, despite the fact that it is stated in purely religious terms. In particular, the prediction is that the bee-like behavior of the Hutterites is promoted by a social organization and ideology that nearly eliminates the potential for individuals to increase their fitness relative to others within groups.²⁴ Note that the other two interpretations do not make the same prediction. If Hutterite society is governed by independent cultural forces, it is unlikely to have the specific design features of a group-level vehicle.

And if selflessness is a product of manipulation, we should find fitness differences between the puppets and the puppeteers.

A number of caveats are in order before proceeding. First, we do not claim to distinguish rigorously among the above three explanations within the confines of this target article. The best that we can do is to provide a brief sketch; this is nevertheless important because it makes the preceding discussion less abstract and gives an idea of what a group-level vehicle of selection might look like in humans. Second, we do not regard the Hutterite social organization as a direct product of group selection. Rather, we conjecture that group selection has operated throughout human history, endowing the human psyche with the ability to construct and live within group-level vehicles of the sort exhibited by the Hutterites.²⁵ This enables us to make another prediction – that the Hutterite social organization is not unique but represents a fairly common type of social organization in ancestral environments. Otherwise it could not be interpreted as an evolved adaptation. As one of many possible social organizations in the human repertoire, this one is presumably evoked only under appropriate environmental conditions, thus yielding another set of testable predictions. Third, evolutionary psychologists rely on fitness-maximizing arguments to explain the human psyche, but they do not necessarily expect humans to maximize biological fitness in present day environments. This is because, to the extent that humans are “programmed” by natural selection, it is not to maximize biological fitness per se but only to achieve the more proximate goals that led to high fitness in ancestral environments. Thus, we must focus more on the design features and what they would have meant in ancestral environments than on the present day consequences of the design features (Symons 1992). This is a general issue in evolutionary psychology that applies to the Hutterites as well as any other group.

With these caveats in mind, we will now elaborate the idea that Hutterite society is a group-level vehicle of selection. Although their ideology is stated in purely religious terms, it is clearly designed to suppress behaviors that benefit some individuals at the expense of others within groups:

That is what Jesus means by His parable of the great banquet and the wedding of the king's son, when the servants were sent to call all the people together. Why did his anger fall on those who had been invited first? Because they let their private, domestic concerns keep them away. Again and again we see that man with his present nature finds it very hard to practice true community; true community feeds the poor every day at breakfast, dinner, and the common supper table. Men hang on to property like caterpillars to a cabbage leaf. Self-will and selfishness constantly stand in the way! (Ehrenpreis 1650/1978, pp. 11–12)

Benefiting the group is exalted as highly as selfishness within groups is reviled:

Where there is no community there is no true love. True love means growth for the whole organism, whose members are all interdependent and serve each other. That is the outward form of the inner working of the Spirit, the organism of the Body governed by Christ. We see the same thing among the bees, who all work with equal zeal gathering honey; none of them hold anything back for selfish needs. They fly hither and yon with the greatest zeal and live in community together.

Not one of them keeps any property for itself. If only we did not love our property and our own will! If only we loved the life of poverty as Jesus showed it, if only we loved obedience to God as much as we love being rich and respected! If only everybody did not hang on to his own will! Then the truth of Christ's death would not appear as foolishness. Instead, it would be the power of God, which saves us. (Ehrenpreis 1650/1978, pp. 12–13)

Thus the Hutterites are as explicit as they can possibly be that their members should merge themselves into a group-level organism. They are also explicit about how group-level functional organization can be accomplished. In the first place, the Hutterites believe that selfishness is an innate part of human nature that can never be fully eradicated:

The sinner lies in all of us; in fact to sin, to be selfish, is our present inclination. Left to ourselves we shall end up in damnation, but this does not mean that salvation cannot be attained. On the contrary, salvation is possible on three conditions: we live according to the life of Christ; we live in community; we strive very hard to attain salvation and are prepared to suffer for our efforts. Christ appeared to save us from our sinful nature. This nature is not easily abjured but it can be if we try hard enough, both in the sense of personal determination and in the sense of collectively living according to the Word. (Shenker 1986, p. 73)

If we were to translate this sentiment into evolutionary language, we would arrive at the claim that within-group selection has been a powerful (but not lone) force in human evolution and has stamped itself upon the human psyche. To the extent that humans are the products of natural selection, they are inclined to benefit themselves at the expense of others within their groups whenever it is evolutionarily advantageous to do so (at least in ancestral environments). To create a group-level organism, the part of human nature that has evolved by within-group selection must be constrained by a social organization that plays the same functional role as the genetic rules of meiosis.

The most important ingredient of this social organization is evidently a sense of “shared fate”:

The community can “hang together” only through the members having an identity of fate. In practice this means two things. Members must identify with the past and (more important) with the future of the community, such that their own future and the community's future are one and the same. We rise and fall together. This is another way of saying we have unconditional commitment to our community. We do not say “if the community does or achieves such and such, then I will stay, otherwise I won't,” since this implies that there is an individual identity ontologically and morally distinct from the community's. No true community could operate successfully or manifest its *raison d'être* with such limiting conditions or separate identities. Identity of fate also means that members relate to each other in an atmosphere of mutual trust, i.e. they consider their presence to stem from a common desire to express their humanity and recognize that this can only be achieved through mutual effort. Should one person claim that he has an inherent right to gain for himself at the expense of others, the entire fabric collapses. Life in the community presupposes that each will work for the benefit of others as much as for himself, that no-one will be egoistic. The moment this assumption is undermined, mutual suspicion, jealousy and mistrust arise. Not only will people probably consider themselves silly for being self-righteous while others are feathering their nest, but operationally the

community will have to take a different character (primarily through the use of coercion) and the entire moral nature of the community disappears. (Shenker 1986, p. 93)

We could not ask for a stronger correspondence between the sentiment expressed in this passage and the concept of vehicles in a group selection model.

One way to establish a sense of shared fate is via egalitarian social conventions that make it difficult for one to benefit at the expense of others. Hutterite society is elaborately organized along these lines. In addition to practicing community of goods, they discourage individuality of any sort, for example, in the context of personal appearance and home furnishings. Leaders are elected democratically and are subject to long probationary periods before they are given their full authority. The Hutterites' passion for fairness is perhaps best illustrated by the rules that surround the fissioning process. Like a honeybee colony, Hutterite brotherhoods split when they attain a large size, with one half remaining at the original site and the other half moving to a new site that has been preselected and prepared. In preparation for the split, the colony is divided into two groups that are equal with respect to number, age, sex, skills, and personal compatibility. The entire colony packs its belongings and one of the lists is drawn by lottery on the day of the split. The similarity to the genetic rules of meiosis could hardly be more complete.

In principle, we might imagine that a psychological egoist, who thinks only in terms of personal gain, could decide to become a Hutterite if he became convinced that the group-level benefits (which he shares) are sufficiently great and the social conventions are sufficiently strong that neither he nor anyone else in the group can act as a freeloader. The Shenker passage just quoted suggests, however, that an effective group-oriented society cannot be composed of individuals who are motivated solely by a calculus of self-interest.²⁶ The external social conventions that make freeloading difficult are evidently necessary but not sufficient and must be supplemented by a psychological attitude of genuine concern for others; a direct calculus of group-interest rather than self-interest is essential. Recall that Simon (1991) makes a similar point about the behavior of individuals in business organizations. Thus, although we are focusing on the Hutterites, our discussion is not limited to esoteric communal societies, a point to which we will return below.

Even with these attitudes and social conventions, however, selfishness in thought and action cannot be eliminated entirely. The Hutterites, therefore, have a well-specified procedure for dealing with members who benefit themselves at the expense of others.

The bond of love is kept pure and intact by the correction of the Holy Spirit. People who are burdened with vices that spread and corrupt can have no part in it. This harmonious fellowship excludes any who are not part of the unanimous spirit. . . . If a man hardens himself in rebellion, the extreme step of separation is unavoidable. Otherwise the whole community would be dragged into his sin and become party to it. . . . The Apostle Paul therefore says, "Drive out the wicked person from among you."

In the case of minor transgressions, this discipline consists of simple brotherly admonition. If anyone has acted wrongly toward another but has not committed a gross sin, a rebuke and warning is enough. But if a brother or a sister obstinately resists brotherly correction and helpful advice, then even

these relatively small things have to be brought openly before the Church. If that brother is ready to listen to the Church and allow himself to be set straight, the right way to deal with the situation will be shown. Everything will be cleared up. But if he persists in his stubbornness and refuses to listen even to the Church, then there is only one answer in this situation, and that is to cut him off and exclude him. It is better for someone with a heart full of poison to be cut off than for the entire Church to be brought into confusion or blemished.

The whole aim of this order of discipline, however, is not exclusion but a change of heart. It is not applied for a brother's ruin, even when he has fallen into flagrant sin, into besmirching sins of impurity, which make him deeply guilty before God. For the sake of example and warning, the truth must in this case be declared openly and brought to light before the Church. Even then such a brother should hold on to his hope and his faith. He should not go away and leave everything but should accept and bear what is put upon him by the Church. He should earnestly repent, no matter how many tears it may cost him or how much suffering it may involve. At the right time, when he is repentant, those who are united in the Church pray for him, and all of Heaven rejoices with them. After he has shown genuine repentance, he is received back with great joy in a meeting of the whole Church. They unanimously intercede for him that his sins need never be thought of again but are forgiven and removed forever. (Ehrenpreis 1650/1978, pp. 66–69)

We could not ask for a more explicit awareness of the freeloader problem and what to do about it, including the elements of retaliation and forgiveness that are also part of the tit-for-tat strategy in dyadic interactions. If we were to translate this passage into evolutionary language, it would be as follows: altruism can succeed only by segregating itself from selfishness. Not only does the selfish individual have the highest fitness within groups, but his mere presence signifies a population structure that favors within-group selection, causing others quickly to abandon their own altruistic strategy. Fortunately, in face-to-face groups whose members are intimately familiar with each other, it is easy to detect overt forms of selfishness and exclude the offender. When "subversion from within" can be prevented to this extent, extreme altruism, in both thought and action, becomes evolutionarily advantageous.

It is remarkable, and crucial for the hypothesis under consideration, that the willingness of the Hutterites to sacrifice for others is accompanied by such an elaborate set of rules that protect self-sacrifice from exploitation within groups. We suggest that there is a causal relationship here, that humans are inclined to adopt selfless behavior in social organizations that provide the functional equivalent of the genetic rules of meiosis. Not only do these social organizations promote selflessness at the behavioral level, but they also promote forms of thinking and feeling that would be classified as non-egoistic in a psychological sense. After all, what is the advantage of psychological selfishness if the most successful way to behave is by contributing to group-level functional organization?

It is also crucial for our hypothesis that group-level functional organization is, in some sense, superior to what can be accomplished by individuals when they are free to pursue their own self-interest (recall the Seeley passage quoted in sect. 2, para. 1). This certainly appears to be the case for the Hutterites, who do not have to wait for the hereafter to get their reward. By fostering a selfless

attitude towards others and minimizing the potential for exploitation within groups, they are spectacularly successful at the group level. In sixteenth century Europe they were alternately tolerated and persecuted for their economic superiority, much like the Jews – another society that, in its traditional form, is well-organized at the group level (MacDonald 1994). In present-day Canada, Hutterites thrive in marginal farming habitats without the benefit of modern technology and almost certainly would displace the non-Hutterite population in the absence of laws that restrict their expansion. The Hutterites' success can also be measured in reproductive terms, since they have the highest birth rate of any known human society (Cook 1954).²⁷ Finally, Hutterite society is internally stable, with the majority of young people electing to remain when given a choice. Were it not for persecution and legal restrictions imposed by their host nations, Hutterite colonies would be far more common than they are now.

Part of our hypothesis is that the Hutterite social organization is not a unique product of the sixteenth century but reflects an evolved human potential to construct and live within such group-level vehicles. It might seem that the Hutterites are such an esoteric society that our prediction could not possibly be confirmed. On closer reflection, however, it appears that the functional elements of Hutterite society that act as group-level rules of meiosis are repeated in a great many social groups that place a premium on group-level performance, even though the ideologies are superficially different and the purpose of the group can be diametrically opposed to the goals of the Hutterites (e.g., an elite military group). Furthermore, according to Knauft (1991), this kind of egalitarianism characterizes hunter-gatherer groups whenever resources are too widely dispersed to allow the development of status-based societies (i.e., most human groups throughout human evolutionary history). The ethic of "good company" (which is extended to nonkin as well as kin; see Knauft 1985) and the deemphasized sense of self-interest that pervades many tribal societies does indeed resemble the Hutterite's "community" and their denigration of "self-will."

Another part of our hypothesis is that the human potential to build and live within group-level vehicles is facultative and evoked more strongly in some situations than in others. Group-level vehicles should be most commonly observed in situations that place a premium on group-level functional organization, such as extreme physical environments, extreme persecution, or extreme intergroup competition. In more benign situations, the consequences of social dilemmas are not so dysfunctional and the effort that goes into the maintenance of group-level vehicles may be correspondingly relaxed.²⁸

Obviously, we have only skimmed the surface of an enormously complex and poorly understood subject. We hope we have demonstrated the likelihood, however, that group selection in humans extends far beyond nepotism and narrow reciprocity. These two principles cannot account for the full range of prosocial behaviors in humans, and evolutionists who rely on them have been forced to invoke other factors, such as that prosocial behavior evolved in ancestral groups of closely related individuals and is maladaptively expressed in modern groups of unrelated individuals (Ruse 1986), that prosocial behavior

is a form of manipulation whereby some individuals profit at the expense of others (Dawkins 1982a; 1989), or that prosocial behavior results from cultural forces that promote biologically maladaptive behavior (Campbell 1983). Group selection theory provides a robust alternative: even large groups of unrelated individuals can be organized in a way that makes genuinely prosocial behavior advantageous.

We have emphasized group-level functional organization in humans as an antidote to the rampant individualism we see in the human behavioral sciences, but it is not our goal to replace one caricature with another. Many human groups are clearly not the "organisms" that we have described above and must be explained as the product of conflicting individual interests within the group. Evolutionary theory has the resources to understand both conflict and cooperation. Only by pursuing both problems – with the group as well as the individual as possible units of functional integration – can the human sciences come to terms with our evolutionary heritage.

3. Conclusions

Maynard Smith's most recent comment on group selection includes the following passage:

It is . . . perfectly justified to study eyes (or, for that matter, ribosomes, or foraging behaviors) on the assumption that these organs adapt organisms for survival and reproduction. But it would not be justified to study the fighting behavior of spiders on the assumption that this behavior evolved because it ensures the survival of the species, or to study the behavior of earthworms on the assumption that it evolved because it improves the efficacy of the ecosystem. (Maynard Smith 1987b, p. 147)

Maynard Smith still resists what we think is the most fundamental implication of natural selection as a hierarchical process: higher units of the biological hierarchy can be organisms, in exactly the same sense that individuals are organisms, to the extent that they are vehicles of selection. Group organisms may be less common than individual organisms and they may be more vulnerable than individuals to subversion from within, but this must not prevent us from recognizing group-level functional organization where it exists.

As the most facultative species on earth, humans have the behavioral potential to span the full continuum from organ to organism, depending on the situations we encounter and the social organizations that we build for ourselves. We often see ourselves as "organs." We sometimes identify ourselves primarily as members of a group and willingly make sacrifices for the welfare of our group. We long to be part of something larger than ourselves. We have a passion for building, maintaining, and abiding by fair social organizations. The individualistic perspective seems to make all of this invisible. Because group-level functional organization can be *successful*, it is labelled *selfish*, and therefore no different from the kinds of behaviors that succeed by disrupting group-level functional organization. But this is just a conjurer's trick. There are compelling intellectual and practical reasons to distinguish between behaviors that succeed by contributing to group-level organization and behaviors that succeed by disrupting group-level organization. That is what the words "selfish" and "unselfish," "moral" and

"immoral" are all about in everyday language. Human behavioral scientists need to focus on these ancient concerns rather than obscuring them with overextended definitions of "self-interest." A concern for within-group versus between-group processes characterizes the human mind and should characterize the study of the human mind as well.

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NOTES

1. In this target article we use the word "individual" to refer to a single flesh-and-blood creature, such as a bird or a butterfly. We use the term "organism" to refer to any biological entity whose parts have evolved to function in a harmonious and coordinated fashion.

2. The purpose of this table is to provide a reasonably complete guide to the modern literature on group selection. A number of controversies exist within this literature that are beyond the scope of this target article. For completeness we provide references for all sides of these controversies, including those with which we disagree. The philosophical literature on levels of selection has recently been reviewed by Sober and Wilson (1994).

3. Williams was only one of many biologists who reacted against group selection during the 1960s, especially in response to Wynne-Edwards's (1962) *Animal dispersion in relation to social behavior*. We do not mean to imply that Williams was the only articulate critic, but he has become the icon for the individualistic perspective in biology.

4. Dawkins (1982a; 1989) acknowledges that the group selection controversy is a "vehicle" question but asserts that groups are almost never vehicles of selection, with the possible exception of the eusocial insects. Dawkins (1989, pp. 297–98), and Cronin (1991, p. 290) cite Grafen (1984) as the authoritative critique of group selection, but Grafen's treatment of groups as vehicles consists of a single parenthetical statement (p. 76): "(The organismal approach suggested here is not in conflict with the 'gene selectionism' of Dawkins [1982a; 1982b]. In his language, we are saying that the individual is usually a well-adapted vehicle for gene replication, while groups are usually not.)" Williams (1986, p. 8) states that "Selection at any level above the family (group selection in a broad sense) is unimportant for the origin and maintenance of adaptation. I reach this conclusion by simple inspection." More recently, Williams (1992) has acknowledged that groups are vehicles in the specific cases of eusocial insects and female-biased sex ratio, but he has not generalized to other cases.

5. Cronin's (1991) *The ant and the peacock* belongs to the same genre as Dawkins's (1976) *The selfish gene* and Gould's (1989) *Wonderful life* in which the author attempts to make the subject accessible to a popular audience without sacrificing scholarship. As Gould (1989, p. 16) put it, "we can still have a genre of scientific books suitable for and accessible alike to professionals and interested laypeople." Because these books are so accessible, they tend to be influential even among academic audiences, which is why Cronin's (1991) work merits criticism despite its status as a "popular" book. Similar views can be found in the more technical gene-centered literature (see references in note 4).

6. Gould (1992) criticizes Cronin's gene-centered approach and advocates a hierarchical view of evolution. However, he accepts the gene-centered framework for the evolution of altruism and does not invoke the concept of vehicles in the same sense that we do. More generally, the concept of "species selection" that Gould emphasizes is somewhat different from

the concept of group selection that we review here (for a discussion of the difference, see Sober 1984). This constitutes one of the controversies within the group selection literature mentioned in note 1.

7. The term "unit of selection" has become ambiguous because it refers to both replicators and vehicles, depending on the author. Within the group selection literature, "unit" equals "vehicle" and no word is required for "replicator" because it is (and always was) assumed that natural selection at all levels results in gene-frequency change. We prefer the word "unit" but use the word "vehicle" in this paper to distinguish it from replicator and also to force gene-centered theorists to acknowledge the implications of their own framework.

8. We start at the lowest level and work up the hierarchy for convenience, not because it is required for the procedure. Also, unless there is uncertainty as to where fitness differences are occurring, it is not necessary to invoke Williams's (1966) concept of parsimony in this procedure.

9. Even though organisms are defined on the basis of functional coordination among their parts, functional coordination per se does not enter into our definition of vehicles, which is based purely on shared fate. This is because shared fate is the crucial property of the process of natural selection; functional coordination among the parts is a product of the process.

10. The procedure for identifying vehicles requires some precautions that can be illustrated by the following examples. First, imagine that tall individuals are fitter than short individuals regardless of how they are structured into groups. The procedure will (correctly) identify the individual as the vehicle of selection. Nevertheless, groups that contain more tall individuals than other groups will be more productive, suggesting (incorrectly) that groups are also vehicles of selection. To resolve this difficulty we must imagine placing all individuals in a single group. Tall individuals are still fittest, demonstrating that the metapopulation structure is irrelevant. As a second example, imagine that the fitness of everyone in a group is directly proportional to the average height of the group. Our procedure (correctly) identifies the group as the vehicle of selection because there are no fitness differences between individuals within groups. To confirm this result, imagine placing all individuals in the same group. The fitness of tall and short individuals is identical, demonstrating that the metapopulation structure is necessary for tallness to evolve (Sober 1984; see also, Goodnight et al. 1992; Heisler & Damuth 1987; Walton 1991). Another problem arises when a trait has already evolved to fixation. To apply the procedure we must conduct a thought experiment (or a real experiment) in which alternative types are present. Although other refinements in our procedure may be needed, these do not require discussion in the present context.

11. Although female-biased sex ratios evolve by group selection, they cannot be used to assess the importance of group selection in the evolution of other traits. In other words, it does not follow that group selection can be ignored for species that have an even sex ratio. This is because the metapopulation structure must be defined separately for each trait (hence the term "trait group"; see D. S. Wilson 1975; 1977a; 1980). The trait group for sex ratio must persist long enough for $f1$ progeny to mate within the group before dispersing, a constraint that does not necessarily apply to other traits.

12. For most evolutionists, the ultimate rejection is to be labelled "non-Darwinian." In fact, Darwin's (1871) theory for the evolution of human moral sentiments is remarkably similar to the vehicle-based framework that we develop here (Richards 1987).

13. We think that an evolutionary theory of genuine versus apparent psychological altruism is possible, but it must be based on the proximate motivations of the actor, which evolutionary accounts ignore by defining altruism and selfishness solely in terms of fitness effects. In other words, we must ask questions such as, When are the behaviors motivated by a "genuinely"

psychologically altruistic individual more fit than the behaviors motivated by an "apparently" altruistic individual? Frank is actually one of the few authors who are asking these questions, so we are not criticizing his specific proposals about emotions as commitment devices, which make more sense within a vehicle-based framework than within a replicator-based framework. For further discussion, see D. S. Wilson (1992) and Sober (in press).

14. R. H. Frank (1988) anticipates this conclusion in the passage we quote (sect. 1.5, para. 2), but does not pursue it further.

15. Anatol Rapoport, who submitted the tit-for-tat strategy to Axelrod's (1980a; 1980b) computer tournaments, always appreciated its group-level benefit and individual-level disadvantage (e.g., Rapoport 1991). In contrast, Axelrod and the majority of evolutionary game theorists regard tit-for-tat as a strategy that succeeds "at the individual level."

16. Sterelny and Kitcher (1988) recognize that Dawkins's position cannot simply be the empty truism that evolution occurs when the genetic composition of a population changes. They claim (p. 340) that the nontrivial thesis that Dawkins advances is that "evolution under natural selection is thus a process in which, barring complications, the average ability of the genes in the gene pool to leave copies of themselves increases with time."

Although this is a nontrivial claim, it is not something we find in Dawkins's writings, and in any case it isn't true as a generality. The average fitness of the alleles at a locus increases under frequency-independent selection. But when a truly selfish gene replaces an altruistic allele, the effect is to reduce average fitness. Dawkins frequently remarks that there is nothing to prevent natural selection (meaning within-group selection) from driving a population straight to extinction. It is also worth noting that group selection can lead the average fitness of the selected alleles to increase. A gene's ability to leave copies of itself can decline under selection, as well as increase. And which turns out to occur is a separate issue from whether group selection is present or absent.

17. Just as group selection has been a controversial topic within biology, the entire subject of evolution has been a controversial topic when applied to human behavior. There are at least three ways that evolution in general (and group selection in particular) can influence human behavior. First, the psychological mechanisms that govern human behavior can be the product of natural selection. In its weak form this statement is uncontroversial, since everyone agrees that basic drives such as hunger, sex, and pain exist because they are biologically adaptive. Some psychologists believe that the adaptationist program can be used to explain the architecture of human cognition in much greater detail, however, and this position is more controversial (e.g., Barkow et al. 1992). Second, cultural change can itself be described as an evolutionary process with between- and within-group components (e.g., Boyd & Richerson 1985; Findlay 1992). Third, genetic evolution is an ongoing process that can partially explain differences between individuals and populations. Our own thinking is based primarily on the first and second influences. In other words, we think it is imperative to explore the hypothesis that group selection was a strong force during human evolution, resulting in proximate psychological mechanisms that are today universally shared and that allow humans to facultatively adopt group-level adaptations under appropriate conditions. The specific nature and precision of these psychological mechanisms are empirical issues. We also propose, along with Boyd and Richerson (1985) and Findlay (1992), that group selection can be a strong force in cultural evolution. Thus, our position is compatible with, but does not require, a strong form of human sociobiology. Our point is not to prejudge the correctness of adaptationist explanations, but to urge the importance of asking adaptationist questions. Only by doing so can we find out whether and to what degree organisms are well adapted to their environments (Orzack & Sober 1994).

18. Sober (1981) discusses the relationship between methodological individualism and the units of selection controversy in more detail.

19. Opportunity levelling is not restricted to the largest human groups. According to Knauff (1991), the simplest human societies are highly egalitarian and overtly status-oriented societies require a concentrated and stable resource, such as crops or livestock. This improves Alexander's general thesis, especially if the simplest existing human societies represent ancestral conditions.

20. Alexander's views on group selection, presented in articles and books from 1974 to 1993, are difficult to represent in a single passage. When evaluating group selection in nonhuman species, Alexander identifies strongly with the views of Williams and Dawkins, as the passage quoted in section 1.2, paragraph 7 shows. Alexander does speculate that humans may be an exception to the rule because of extreme between-group competition and regulation of fitness differences within groups. The following passage illustrates his pro-group selection side, which is consistent with our own interpretation: "In sexually reproducing organisms, such as humans, confluentes of interest within groups are likely to occur when different groups are in more or less direct competition. As a result, the kind of selection alluded to here [group selection] would be expected to produce individuals that would cooperate intensively and complexly *within* groups but show strong and even extreme aggressiveness *between* groups (Alexander 1989, p. 463). However, in other passages, Alexander clearly minimizes the importance of group selection and attributes the evolution of moral behavior in humans to within-group processes. We provide his most recent statement to this effect: "Because selection is primarily effective at and below the individual level, it is reasonable to expect concepts and practices pertaining to morality – as with all other aspects of the phenotypes of living forms – to be designed so as to yield reproductive (genetic) gains to the individuals exhibiting them, at least in the environments of history" (Alexander 1993, p. 178).

At a more technical level, Alexander occasionally seems to appreciate the vehicle concept when evaluating levels of selection (e.g., the 1989 passage quoted above), but more often he implicitly defines anything that evolves as "individually" advantageous, even when the group is the vehicle of selection (e.g., Alexander's 1993 discussion of R. H. Frank [1988]). We think that a consistent application of our procedure will reveal that Alexander is invoking groups as vehicles of selection much more than he acknowledges in his own writing. We also want to stress, however, that Alexander's views on indirect reciprocity, opportunity-leveling within groups, and competition between groups remain important within a vehicle-based framework.

21. Alexander's theory is conventional in the sense of equating morality with the notion of a common good. However, calling it familiar and conventional does not belittle its importance. Evolutionary theories of human behavior frequently make predictions that correspond closely to folk psychology (e.g., that men tend to value youth in women more than women value youth in men; see Buss: "Sex Differences in Human Mate Preferences" *BBS* 12 (1) 1989; Kenrick & Keefe: "Age Preferences in Mates Reflect Sex Differences in Human Reproductive Strategies" *BBS* 15 (1) 1992). Since the intuitions of folk psychology are unlikely to be completely wrong, it would be disturbing if an evolutionary theory of human behavior were not familiar and conventional in some sense. Of course, the theory must also go beyond folk psychology by making counterintuitive predictions, revealing aspects of folk psychology that are false, refining familiar predictions, subjecting predictions to empirical test, and so on.

An evolutionary account of morality (including Alexander's) does depart from folk psychology in some important respects. The organ-organism-population trichotomy implies that there will always be a level of the biological hierarchy at which social

dilemmas will prevail. In other words, moral behavior within groups will frequently be used to generate immoral behavior between groups. This fits well with observed behavior but contrasts with the concept of universal morality that is common in folk psychology and some branches of the human behavioral sciences (e.g., the higher stages of Kohlberg's [1984] theory of moral development; MacDonald 1988b). In addition, if moral systems function as group-level rules of meiosis, it becomes difficult to explain the concept of individual rights, which are moral rules that protect individuals from groups. We think that an evolutionary account of morality may ultimately shed light on these topics but it will need to be more sophisticated than current accounts.

22. We provide Alexander's most recent statement that humans are motivated entirely by self-interest: "It is not easy for anyone to believe, from his own thoughts about his personal motivation and that of other humans, that humans are designed by natural selection to seek their own interests, let alone maximize their own genetic reproduction" (Alexander 1993, pp. 191–92).

23. The invisible hand metaphor is the economic equivalent of the Gaia hypothesis. More generally, despite its emphasis on individual self-interest, economic theory is like naive group selection in its axiomatic belief that multi-individual firms maximize a collective utility. A more sophisticated hierarchical approach to economics, along the lines of Campbell (1993), Leibenstein (1976), Margolis (1982), and Simon (1991) will be highly interesting.

24. The sense in which we expect an absence of fitness differences within groups needs to be clarified. In honeybee colonies, there is a set of adaptations that is favored by within-colony selection and has the potential of disrupting colony function. This includes workers laying unfertilized eggs to produce sons and workers favoring their own patriline while tending future queens. These behaviors are seldom observed because of evolved adaptations that prevent them, which qualify as group-level rules of meiosis (Ratnieks 1988). Another set of adaptations is favored by within-colony selection but does not disrupt colony function. For example, a beneficial mutation that increases viability will cause patrilines that have this mutation to be more fit than patrilines that don't, but there is no reason to expect these kinds of fitness differences to be suppressed by group-level rules of meiosis. Similarly, we expect the Hutterite social organization to suppress fitness differences that correspond to the first set but not those that correspond to the second.

25. Here we are following Tooby and Cosmides' (1992) concept of modularity, according to which natural selection has evolved a number of cognitive subsystems that are evoked by appropriate environmental conditions. We do not however, mean to exclude the possibility of open-ended learning and cultural evolution, as envisioned by other evolutionary psychologists (e.g., Boyd & Richerson 1985; Durham 1991; MacDonald 1991).

26. Two caveats are in order here. First, people do not necessarily think the way an ideology exhorts them to think. We believe it plausible that Shenker (who was himself an Israeli kibbutznik) is not simply espousing an ideology but is accurately describing the attitudes and beliefs that exist among members of communal societies. Second, psychological egoism can be defined in many ways and some of the broadest definitions would include the attitudes and beliefs expressed in the Shenker passage. For example, if a Hutterite takes genuine pleasure in helping his group, he might be classified by some as a psychological egoist who is attempting to maximize his pleasure. For the purposes of this discussion, we define a psychological egoist as a person who has a category of "self" that is separate from the category of "others," who acts to maximize perceived self-interest without regard to effects on others, and who does not axiomatically find pleasure in helping others. See Batson (1991) for more detailed discussions of psychological egoism.

27. Although the evaluation of psychological adaptations should be based on design features and their reproductive consequences in ancestral environments, it is still interesting to examine the reproductive consequences in modern environments. The Hutterites have been quite well studied demographically and it should be possible to measure actual fitness differentials within groups.

28. In addition to the environmental situations that we have listed, unstable equilibria leading to majority effects are likely to be important in the evolution and maintenance of group-level adaptations. In other words, group-level adaptations may have difficulty evolving from a low frequency even when they are favored by environmental conditions. Conversely, after they have become established, group-level adaptations may persist even after the environmental conditions that favored them are relaxed (Boyd & Richerson 1990a).

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Driving both ways: Wilson & Sober's conflicting criteria for the identification of groups as vehicles of selection

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Abstract: We argue, first, that the notion of group selection discussed in Wilson & Sober's target article is much stronger than that in Sober (1984). Next, we show that the authors are tacitly using two independent criteria in applying this notion, a "differential fitness" criterion and a "shared fate" criterion. These criteria are flawed and cannot be applied jointly to the cases Wilson & Sober describe without creating inconsistencies.

We will focus here on Wilson & Sober's (W & S's) specifically biological claims. If W & S's vision of group selection in biology is as deeply flawed as we will argue, the details of their arguments with respect to sociobiology are fully beside the point.

W & S base their ideas about group selection on the "vehicles of selection" concept, that is, Hull's (1981) notion of evolutionary "interactors." We will attempt to extract a precise notion of "vehicle" from their account. Our main points will be that W & S are committed to this notion; that there are two completely independent interpretations of it; and that each interpretation is appropriate for at least one of their major examples. Furthermore, if W & S wish to distinguish group selection from kin selection or evolutionary game theory on the one hand, and from fanciful Gaia hypotheses on the other, *both* interpretations are indispensable. Since they yield different results, however, this duality makes it impossible for W & S to make any generalizations about the status of group selection theory in biology or its potential applications to sociobiology.

Our first task is to show that W & S go beyond a "weak" formulation of group selection, one that was outlined coherently in earlier work by Sober (1984, p. 314): "group selection occurs . . . exactly when there exists some property P such that

(1) Groups vary with respect to whether they have P, and (2) There is a common causal influence on those groups that makes it the case that (3) Being in a group that has P is a positive causal factor in the survival and reproduction of organisms." In other words, group selection occurs whenever individual fate is affected in any way by group membership for any reasons that are causally interpretable.

The main evidence that W & S have abandoned this "weak" definition is provided by their repeated use of a "simple procedure" for identifying "vehicles," that of "frameshifting" among levels of the biological hierarchy.

Starting at the lowest level of the hierarchy, ask the question "Do genes within a single individual differ in fitness?" If the answer is "no," then they share the same fate and are part of the same vehicle. Proceeding up the hierarchy, ask the question "Do individuals within a single group differ in fitness?" If the answer is "no," then once again they share the same fate and we must proceed up the hierarchy until we find the level(s) at which units differ in fitness. This is the level (or levels) at which natural selection actually operates, producing the functional organization implicit in the word "organism." (sect. 1.4) Frameshifting requires an important assumption: selection occurs at a level if and only if entities at that level differ in their "fitness." There is no question that this is what W & S mean because they use the term "fitness" repeatedly in each discussion of frameshifting.

Can the above procedure be derived from Sober's "weak" definition? We can see no clear relationship between the requirements that group membership influence individual fitness and that groups themselves differ in their fitnesses. Instead, we see two rather different interpretations, each implying that much stronger conditions are necessary for group selection. The first is relatively straightforward, and is in fact the first to be discussed by W & S. Groups are treated as "individuals" with well-defined "births," "deaths," and "descendants" that inherit characteristics. The second interpretation, to be discussed shortly, focuses on W & S's suggestion that individual members of a population subject to group selection "share the same fate."

Beyond any purely suggestive "functional organization implicit in the word organism," why must we treat groups as individuals with organism-like properties? We need only reflect on the role of fitness in W & S's vehicle-identifying procedure. At each level of the procedure, the candidate vehicle must minimally be the sort of thing to which fitness can be ascribed. In turn, fitness must be cashed out in terms of reproductive success, which requires that the entity in question (in this case, a group) be capable of reproduction. In other words, a group must be like an individual organism in having "births," "descendants," and the like.

The first two important cases discussed by W & S both accord well with this interpretation. In the hypothetical case of island-dwelling rabbits, island colonization = birth; colony extinction = death; new colonies produced by dispersal among islands = descendants; and colonies can inherit gene frequencies from their ancestors. Similar equivalences apply in the case of social insects.

If W & S were content to define group selection as a result of the differential reproduction of groups, they would be hard-pressed to argue for group selection in numerous cases where one or another criterion for group-level reproduction is not met. In fact, at first glance, few of these conditions seem to be met by the "groups" dealt with by evolutionary game theorists. This is a serious problem because W & S feel compelled to show that inclusive fitness and evolutionary game theory merely describe special cases of group selection. This claim does in fact follow easily from Sober's earlier "weak" notion of group selection, but we will argue that it does not follow at all from the "differential fitness" criterion.

A good example of the kind of group that might be of interest to an evolutionary game theorist is that of sibgroups. W & S claim that "sibgroups with more altruists outproduce sibgroups

with fewer altruists" (sect. 1.5). However, there is no clear sense in which sibgroups "reproduce." This is because no particular sibgroup in a preceding generation can be identified as the "ancestor" of any succeeding sibgroup. W & S disavow "identity by descent" as a necessary condition for selection, but this has no bearing on the issue of whether patterns of descent can be traced from one group-level "generation" to the next, which seems to us like a minimal requirement for defining reproduction.

W & S do seem aware of this problem. Consider their dismissal of the "only discrepancy" between kin selection and group selection accounts in the case of sibling groups, which "involves the concept of extinction":

Sibling groups don't last for multiple generations and don't necessarily go extinct, but rather dissolve into the larger population when the individuals become adults and have their own offspring. Thus, sibling groups (and social insect colonies) differ somewhat from our population of rabbits and the groups that Frank and Trivers had in mind. But this does not disqualify sibling groups as vehicles of selection. After all, individuals are transient collections of genes that "dissolve" into the gene pool as gametes. (sect. 1.5)

But when we consider the analogy more carefully, it appears highly misleading. Individuals are collections of genes, just as sibgroups are collections of individuals. However, the production of gametes by diploid individuals does not involve a shift among levels analogous to the dissolution of sibgroups because gametes, as haploid individuals, are at exactly the same organizational level as their diploid parents. Calling haploid individuals "gametes" does not transform them somehow into loose federations of independently selected genes. Instead, the ancestor-descendant relationships among "individuals" (diploids), "gametes" (haploids), and the resulting second-generation "individuals" are crystal clear, because all of these entities are at the same level.

Sibgroups are not the only example cited by W & S that fails to meet the differential fitness notion of groups as individuals. The "cricket boatmen" example also concerns "ephemeral" groups. W & S claim that "persistence is a requirement for replicators, not vehicles," (sect. 1.6) but the important sense in which these groups are ephemeral is once again that they are incapable of participating in specific ancestor-descendant relationships. Unlike organisms in which diploid individuals directly produce haploid individuals and vice versa, the cricket boats "produce" a population of surviving crickets that itself produces a new generation of crickets, which only then is organized into new cricket boats.

To deal with the inadequacy of the differential fitness criterion in cases like these, W & S implicitly shift to what we consider a second, discrete interpretation of their own vehicle-identifying procedure: if individuals have a "shared fate" with respect to survival and reproduction, the groups they form are vehicles of selection. Of course, if shared fate really was just an epiphenomenon of differential fitness, we could conclude immediately that frameshifting just does not work on examples drawn from evolutionary game theory, invalidating W & S's entire thesis. There is good evidence for this claim, because the authors repeatedly argue that if there is any differential fitness at, say, the level of individuals within groups, there must be both a sharing of fate and selection at the individual level.

One is tempted to conclude that, for W & S, shared fate is the true necessary and sufficient condition for group selection, and talk of differential fitness is mere window-dressing. This would be extremely convenient. Consider the example of the cricket boats, which has just been shown not to be interpretable in terms of differential fitness. In the simple case of fully cooperating cricket diads, individual survival (and implicitly fitness) is entirely determined by the success or failure of a boat's efforts to find lily pads. There could be no more unambiguous case of shared fate, which presumably explains why W & S are eager to say that examples like this prove that evolutionary game theory is a special case of group selection.

Unfortunately, the notion of shared fate does not appear to apply nearly as strongly to W & S's earlier examples of rabbits and social insects as it does to cooperating cricket boatmen. When an island colony of rabbits reproduces by dispersal to a new island, only a distinct subset of the colony's rabbits become founders of the new population, and even within that subset fitnesses differ. Hence, the "shared fate" requirement appears to be weakened in not one but two different ways: individual rabbits differ in their chances of belonging to the founder group *and* in their reproductive success relative to other founders. Social insects are exactly the same because the vast majority of genetically distinct individuals are nonreproducing workers.

The easiest way to account for this discrepancy would be to reinterpret the shared fate criterion as nothing more than a euphemism for Sober's (1984) definition of group selection as any selection process in which group membership influences individual fitness, but this cannot be W & S's intention, given their reliance on the frameshifting paradigm. Alternatively, W & S might try to show that the fitnesses of individual rabbits or insects really are more or less equal by retreating to an argument based on inclusive fitness accounting. However, the sharing of fate within groups would then be described in terms of kin selection – not the other way around!

We have shown that the shared fate criterion must be very weak if it is to apply to cases like that of the rabbits. Nonetheless, W & S need it to claim that group selection is occurring in cases like that of the cricket boatmen, where the differential fitness concept does not apply because the groups do not reproduce in a straightforward manner. There is, however, an even graver problem with the shared fate criterion: just as W & S have implied in their discussion of frameshifting, meeting this criterion alone cannot possibly be sufficient for group selection. Imagine an ecosystem in which all organisms reproduce simultaneously by cloning; there are numerous, well-defined levels of organization; and there is no variation whatsoever in reproductive success. In other words, the ecosystem replicates itself perfectly at each generation. Once again, there could be no more obvious case of shared fate, in this case at any and all organizational levels. Nonetheless, it should be clear that there really is no selection of any kind operating at any of these levels. Hence, the differential fitness criterion is needed after all to explain why cases like these do not involve group selection.

W & S clearly do believe that groups can be identified as vehicles of selection using a coherent procedure based on a single criterion involving both differential fitness and shared fate. However, their application of the procedure to particular examples shows that different criteria are used to argue for group selection in different cases. Although rabbit groups have differential fitness, their components (the individual rabbits) do not have fully shared fates. Cooperating cricket boatmen have fully shared fates, but there is no clear sense in which the dyads "reproduce": only the individuals participate in even marginally identifiable ancestor-descendant relationships.

In summary, Wilson & Sober's account of group selection must be inferred using two fully independent criteria, each of which is highly flawed. The differential fitness criterion helps them to explain selection among discrete populations such as colonies of social insects and, conceivably, of humans. The shared fate criterion makes it possible to treat kin selection and evolutionary game theory as group selection. They need both, but the two fail to yield consistent results when applied to examples. We conclude that W & S's attempt to offer a reconstituted theory of group selection as a foundation for sociobiology should be rejected by students of human behavior.

Seeing the light: What does biology tell us about human social behavior?

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Abstract: Wilson & Sober do not propose a new view of natural selection, but a purification and clarification of the view proclaimed by sociobiologists in the 1970s. Unfortunately, implications for understanding human social behavior remain unclear, resting more on the appearance of connections resulting from shared language than on knowledge of mediating processes.

I am one of those for whom Wilson & Sober's (W & S's) impressive and thought-provoking essay was written – a behavioral scientist interested in what biology can tell us about human social behavior – one who relies on biologists (or biologist watchers) to pass on revelations. Lacking biological expertise, I doubtless do not appreciate all the nuances of the message, and as a seeker after insights W & S can provide, I do not wish to bite the hand that feeds. Still, let me offer a few reactions from the pew. If nothing else, they may reveal how thankless and frustrating missionary work can be, preaching to heathen who have ears but do not hear.

A new gospel? When I first read sociobiologists E. O. Wilson and Dawkins in the mid-1970s, I was impressed by the clear logic and apparent correctness of their argument: the unit of natural selection is not the species, group, or even the individual; it is the gene. One of the strategies genes use in their endless activity of ordering nucleotides into copies of themselves is quite indirect: they join with other genes and use the resources of the environment to produce complex and interdependent organizations – organisms. As the organisms' progeny proliferate, so do the genes.

If I understand W & S aright, they have no quarrel with any of this. Rather, they wish to emphasize that complex and interdependent organizations – organisms – need not always be packaged in one physical body. Higher-level organization can exist in which physical individuals or even collections of physical individuals have specialized functions, as different organs have specialized functions in the body. To the degree that this organization is genetically controlled and subject to reproductive competition, natural selection can occur at the group or even metapopulation level.

Surely this is not a new gospel. It is instead a useful and timely call to (a) turn away from creedal calcification at the individual level, (b) return to fundamental first principles laid down by Williams, E. O. Wilson, Dawkins, and others, and (c) recognize the implications. To counter the excesses of naive group selection, sociobiologists (over)emphasized the infrequency of group selection; to redress the balance, W & S (over)emphasize the frequency. The accent shifts depending on the sin one is preaching against, but the gospel endures.

Lingering doubts. What does this purified and clarified gospel reveal about human social behavior? W & S believe it allows us to conclude that motives directed toward group-interest are a part of human nature, along with motives of self-interest. I remain unconverted. I can agree with W & S that many behavioral scientists have interpreted "selfish-gene" sociobiological arguments as saying far more about human behavior and motivation than is justified, wrongly believing that these arguments provide support for individual self-interest over group interest as motives for human behavior. However, W & S extricate us from this trap only to entice us into another. They would have us believe that their group-level selection arguments say far more about human behavior and motivation than is justified.

Although the terms self-interest, group interest, selfishness, and altruism are used at both the biological and social levels,

they are used quite differently. At the social level, these terms refer to motives, values, intentions, and goals. At the biological level, they refer only to consequences, saying nothing about the nature of the motivation or whether there is any motivation present at all. The shared terminology can lead us to think that what is said at one level has implications for the other.

To be sure, all of our social behavior must be within our genetic repertoire, but that repertoire is vast. Given the complexity and flexibility of the intervening processes, especially of human cognitive processes, most links between our social behavior and genetic makeup remain tenuous and indeterminate. Group interest at the human level, as among the Hutterites, is likely produced by social rather than biological evolution (Campbell 1975). If biological, it could easily be the product of selection at the individual level (e.g., for social docility, Simon 1990; for self-redefinition, Turner 1987; or enlightened self-interest) rather than the group level. Group interest need not be based on group selection, even under conditions that might support group selection. Not every attribute that could evolve by natural selection does, nor is every evolved attribute optimal. Aware of these problems, W & S must fight hard, advancing their group-selection argument on the strength of possibility, then retreating and digging in.

Awaiting the light. Before we can know whether this or other biological arguments shed important light on human social behavior, we need to know far more than we do about the mediating links. Obviously, this is a tall order, although some interesting suggestions have been made (e.g., Frank 1988; Hoffman 1981; Simon 1990).

Thus far, the contribution of sociobiology to understanding human social behavior seems limited to creating, then correcting, premature constraints. Does natural selection constrain us to pursue only personal self-interest? Yes; correct that, no. Does natural selection exclude group selection? Yes; correct that, no. Removing false constraints is certainly useful, but if there are to be more positive human behavioral implications, then some brave souls are going to have to undertake the arduous task of tracing the intermediate steps. Right now, there is no beacon shining from our biology to our social behavior. To see the light, we probably need a little less metaphor and analogy and a lot more science.

The consequences of group selection in a domain without genetic input: Culture

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Abstract: Group selection in humans is principally the product of competition between cultures. Cultures, however, are not directly tied to differences in inherited biological attributes. The result has been, at most, random change, unrelated to differences in adaptive biological characteristics between human groups. Culture, then, is better described as a "domain" than as a "vehicle."

I can add little of direct significance to the thoroughly refreshing and challenging treatment that Wilson & Sober (W & S) have produced. As a scholar who labors at the biological pole of anthropology, I look on with much interest and general approval.

Anthropology has another pole, however, and, because I suspect that there may be a dearth of its representatives among those asked to comment on the issues raised by W & S, I shall attempt to don an ethnological hat and raise what should be an important dimension that is only briefly hinted at in the body of their presentation. This is the matter of "culture" in the anthropological sense. For more than a century, anthropologists have,

either explicitly or tacitly accepted E. B. Tylor's definition of culture as "that complex whole which includes knowledge, belief, art, morals, law, custom, and any other capabilities and habits acquired by man as a member of society" (Tylor 1871, p. 1).

Tylor's definition is of culture in the abstract. Traditionally, ethnologists or "cultural anthropologists" devoted themselves to the study of specific cultures, those bodies of "knowledge, belief, art, morals, law, and custom," and so on, that were manifest in given human populations. Human beings, of course, are quite unable to survive without culture, and, as many have observed, the extraordinary elaboration evident in the cultural realm is one of the most obvious distinctions between the human and the nonhuman. Culture, however, is not a product of the human genome. That was implied when Kroeber (1948, p. 253) called culture "superorganic," noting that it has some of the characteristics of the organic but is in fact something beyond.

The late Leslie White (1959, p. 8) referred to culture as our "extra-somatic adaptation" and treated it as a realm that had undergone its own form of "evolution." This raises the intriguing possibility of studying cultures from the perspective of trying to identify those dimensions that have led to the proliferation of some at the expense of others; but, by and large, ethnologists have tended to shy away from such an approach because of what they regard as the unwelcome specter of determinism. The almost hysterical anthropological reaction to E. O. Wilson's *Sociobiology* (1975) is a case in point (e.g., Sahlins 1976).

For my own part, I have found it useful to treat culture as an ecological niche in itself that has generated selective pressures that have had major consequences in shaping particular aspects of the human biological makeup (Brace 1964, p. 36; 1979, p. 287; 1991, p. 89). In contrast, however, although culture is the product of a broad realm of human mental and linguistic capabilities, there are no particular aspects of culture that are the direct products of specific and inherited biological traits. Differences between human cultures, then, are unrelated to the biological differences between the human groups that have produced them.

The differential survival of those human groups depends completely on the relative success their various cultures have had vis-à-vis each other. Group survival, then, is determined by selection at the cultural level. The record of conflict, conquest, and colonization that can be traced since the Neolithic period clearly shows that group selection has played a major role in the expansion or disappearance of various human populations. It is a form of selection, however, that is completely unrelated to differences in the genetically determined characteristics of the human groups involved. On the other hand, group selection at the cultural level has led to the proliferation of some and the disappearance of other human biological attributes as an accidental byproduct.

One can make the case that group selection in humans has been chiefly the outcome of cultural conflict at least since the origin of the species *sapiens* (possibly over 200,000 years ago), but that it has had no cause-and-effect tie to differences in the inherited biological traits of the populations involved. The survival of genes and individuals was obviously involved but only in inconsequential fashion. The culture or cultures that could be regarded as the elements involved in group selection probably should not be called "vehicles" in W & S's sense, but they would certainly fit into what Williams (1992) means by "domains" when he implicitly accepts the possibility of the hierarchy of units responding to selection that their presentation proposes.

Group selection in the cultural domain has not led to significant biological change in human populations over the last quarter of a million years, but culture has established a barrier between aspects of human biology and particular environmentally expectable selective forces that has allowed genetic

changes to accumulate in certain human groups driven by the accumulation of mutations alone. In an early contribution to the "neutralist" or mislabeled "non-Darwinian" evolutionary outlook, I called the mechanism the Probable Mutation Effect and noted that it could be predicted to work when selection was relaxed or suspended for particular traits (Brace 1963).

Reductions in tooth size can be shown to follow the adoption of specific food-preparation practices (Brace et al. 1991), and reductions of particular aspects of postcranial robustness and muscularity follow the adoption of specific elements of hunting technology (Brace, in press). Unlike the stochastic genetic changes that follow from group selection in the cultural domain, the changes that result from the cultural interposition between the previously expectable aspects of selective force and the phenotype are clearly directional, but they reflect nothing that could be regarded as improved or advantageous in the genetically controlled aspects of the phenotypes of the members of the populations involved.

This is in no way intended to take away from W & S's accomplishments. The point is that the domain of culture can take on a life of its own, with major effects for human survival that are independent of differences in human inherited capabilities. Cultural systems are produced by humans and vie with each other for survival, and this is indeed an obvious example of group selection. The fate of their human creators depends on the success or failure of the culture with which they are associated, but that fate is unrelated to the genetic characteristics of the people involved. Group selection in humans, then, has major implications for cultural evolution but can only produce random and unselected effects on the biological nature of human beings.

Metaphors and mechanisms in vehicle-based selection theory

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Abstract: Vehicle-based approaches to selection are alleged to be superior to replicator-based approaches in that (1) they make room for the legitimacy and importance of group selection and (2) they move from metaphors to mechanisms. I point to some unclarities in Wilson & Sober's concepts of "group" and "group selection" and argue that their vehicle-based approach merely replaces one set of metaphors with another.

In their abstract, Wilson & Sober (W & S) characterize their foil as the view that "social organization is a by-product of self-interest." Later, they castigate the "genic perspective" as failing to address the (implicitly related) key question: "Can groups be like individuals in the harmony and coordination of their parts?" The two issues are not linked in any obvious way. A yes answer to one neither entails nor precludes a yes answer to the other. Groups, in particular, human organizations, may very well be like individuals in the coordination of their parts without being in any clear way the product of group-level selection.

Indeed, there appears to be some ambiguity about how W & S want to understand the concept "group selection." In section 1.2, paragraph 4, they define it in terms of the effects of natural selection (differential increase in groups of a kind), but this is independent of whether adaptations exist at higher levels, which is a prerequisite for natural selection at those levels. This latter characterizes group selection in terms of its causal characteristics. It seems that W & S shift from one perspective to the other and ignore, in effect, Sober's (1984) distinction between "selection of" and "selection for."

In section 1.4, paragraph 4, and later, W & S raise the question of whether there is a relevant analogy between or-

gans/organisms and individuals/groups. Their response is to invoke the view that the "organ/organism/population trichotomy" can be "frameshifted" up and down the biological hierarchy. Even so, that in itself does not show that individuals are in any relevant sense like organs with respect to the groups to which they belong. Even if it is true for some individuals in some groups, it is not true for all individuals or all groups. This weakens the force of the implicit analogy. Frameshifting alone does not suffice. What more is needed? The differences between the functional unity of organs in organisms and the functional unity (such as it is) between individuals and groups needs to be addressed before we can see whether the analogy wrought by frameshifting is apt.

The question of how we are to understand when groups are vehicles is not crystal clear. In their initial characterization (sect. 1.4, para. 3), the key question is whether the entities at a given level have the same fitness and share the same fate. If the answer is "yes," then they are part of the same vehicle. Yet, when the examples of selection at different levels are presented, insect colonies are cited as instances where the colony is a vehicle of selection even though the insects within the colony do not have the same fitness. A similar problem occurs with the "meiotic drive" case or indeed any case where selection is taken to be operating at two different levels. The differences in fitness at the lower level would seem to preclude the entities at that level from being part of the same vehicle in the sense that it is relevant for selection to be operating at the level of the vehicle. I take it that the caveat that fitness is, strictly speaking, a property of traits and not organisms is supposed to take care of this case, but more needs to be said to make it clear how this is supposed to work. Even if we grant W & S their point that selection at the level of group vehicles occurs, it still needs to be shown that any interesting human social organization can be construed as containing individuals with the same fitness who have a shared fate (or who have some trait whose fitness is the same for all in the group).

The main rationale for W & S's target article is to reintroduce group selection to the human behavioral sciences. The fact that some prosocial behaviors can be adaptive (sect. 1.6, para. 11) does not by itself show that there is selection for these prosocial behaviors, that is, that they are adaptations at some higher level. With respect to this last point, we see a recurring theme: Are groups as organisms (*sensu* note 1) entities that are selected for their integrity or is there selection of groups (at least some groups) as a by-product of selection for other factors, for example, individual organisms?

Finally, on the issue of metaphors versus mechanisms, W & S see their approach as replacing mere metaphors with mechanisms. Their own view, however, is itself replete with metaphors: we find, among others, individuals as "populations" of alleles, psychological motives as "game theoretic strategies," and social groups as "organisms." Indeed, the very idea of the "targets" of selection as "vehicles" is a heavily weighted metaphor. In shifting from a focus on replicators to one on vehicles, the authors seek to defuse what they see as potentially misleading and unhelpful metaphors. Focusing on vehicles, however, does not permit escape from the metaphorical web that surrounds theories of selection in biology and the social sciences. It just shifts the focus from one metaphor to another. The image of groups as vehicles – as "carriages" or "rowboats" – brings to mind entities that are subject to causal influence, but what is the actual force of the claim that natural selection operates or occurs at many levels? If we are to understand selection as more than merely the differential proliferation of genes or individuals or groups, then we need to show that groups are "real," as Campbell puts it (sect. 2.2, para. 3). The challenge of Wilson & Sober's piece is to redirect the focus of researchers from genes to levels of organization that may well serve as causal units in selection. This does not avoid metaphors but substitutes one set of metaphors for another.

Group selection and the group mind in science

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Abstract: This plausible group-selection model should aid the conceptual integration of the natural and social sciences, but testing in vertebrates is needed. The history of the vehicles-of-selection debate is compared with the controversy over the readmission of innate behavior and genetics to a respectable position in behavioral study. In the spirit of Wilson & Sober a new "commandment" for the conduct of science is proposed.

This is an important paper both because of its thesis and what it represents for the human behavioral sciences. The consistent vocabulary and effective integration of various lines of argument and evidence greatly advance the case for incorporating groups into selection thinking. A result should be to encourage greater interaction and less acrimony, and certainly more mutual respect, between the social and biological sciences.

Although the basic arguments are not new, the packaging is. Questions remain, however, about the means of obtaining data to test group-selection models. Nonhuman vertebrate work is necessary, and I would like Wilson & Sober (W & S) to outline the kinds of tests they would like to see performed. How should different levels of group effects be handled? The territorial expansion of the Hutterites is, according to W & S, limited by surrounding cultural groups. Is this an indication of relatively lower group fitness? Can we ignore the role of leaders and propaganda in lowering mean fitness (*sensu* Settle 1993) while benefiting oligarchies? Certainly the material condition and reproductive output of surrounding populations appears to be less than that of the Hutterites. Are the surrounding groups subsidized by the metapopulation into which they are more integrated? The discussion of the enigma of group decisions that may be detrimental to every member is relevant in this context, and might lead biologists to reconsider observations noted in such books as *The group mind* (McDougall 1920) as well as more recent social psychology. The recognition that both proximate mechanisms and selective consequences need to be addressed is a strong aspect of W & S's paper; and although the authors focus on the latter, the challenge for the human behavioral sciences has been articulated.

W & S are blunt in recounting the recent history of the group-selection controversy and suggest that the reasons for the resistance to arguments for group selection should be explored. Assuming that W & S (and Emerson's [1960] superorganism institution) are indeed much closer to the truth than those claiming that selection can never act beyond the boundary of the individual, I think one step in such an analysis should be a comparison of this controversy to other seminal periods of conceptual change in the study of behavior. The initial response to, and eventual accommodation of, ethological claims for the necessity of integrating evolution, instinct, and genetic factors into any viable approach to animal behavior provides one such comparison.

Wynne-Edwards (1962) and Tinbergen (1951) each stimulated similar campaigns. Wynne-Edwards's ideas became the focus of attack after kin selection, inclusive fitness, game theory, and other elements collectively provided a simple and elegant explanation for complex social phenomena, especially altruism. This individual-based approach certainly clarified many enigmatic phenomena. It provided a superficially easy-to-understand Darwinian mechanism that some proponents even advanced as obviating the need for empirical study of the associated proximate processes. (After Richard Dawkins made such a claim from the floor at an International Ethological Conference in the

1970s, I left muttering). When evidence showing the limitations of the individual approach began appearing, the response was either to ignore or to dismiss the evidence and models. Now a shift is being seen and a few years from now students may look back in wonder at what the fuss was about. For W & S, group selection does not negate all the processes of individual or even gene selection, but embeds them in a larger matrix of causality.

The initial response of psychologists to ethology, as symbolized by Tinbergen's book, was excitement at the "new" phenomena being studied, but also bewilderment that discarded or trivialized issues of instinct, innate behavior, and genetic determination should once again be allowed to muddy the waters of scientific discourse. In the 1940s, psychologists of several variants of behaviorism were converging on an elegant system of explaining almost any behavior pattern of any species through a combination of reflexes and classical and instrumental (including operant) conditioning. This readily comprehended and clearly articulated set of concepts, vocabulary, and methods provided a rationale for minimizing concern for behavioral, species, and ecological diversity. Although never accepted by all psychologists and confounded with a needlessly naive environmentalism, behaviorism had the scientific panache and approach that promised answers without addressing issues raised by evolutionary processes. Reflecting this behavioristic ethos, many distinguished biologists and psychologists wrote critiques of the ethological heresy. Although some important empirical issues were raised, the punch lines were usually some "logical" (and seemingly irrefutable) point that was thought to effectively derail any reason to bring back concepts such as instinct or the innate. (Support for the broad brush I am wielding can be found elsewhere, e.g., Burghardt 1973, 1985). Ethology never claimed to disprove the existence of conditioning, for example, but did place it in a larger integrated picture, just as W & S are doing here with individual selection! We know what happened in ethology. In 1973 Tinbergen, Lorenz, and von Frisch received the Nobel Prize. Twenty years later, evolution, innate processes, and behavior genetics are central features of human psychology, as documented in the history of this journal. Contemporary ethology has certainly gone far beyond the empirical and conceptual framework of Tinbergen and the early ethologists without disavowing their seminal importance and insights. Perhaps we need to do the same with "naïve" group selection.

Why do scientists continue to treat and defend their ideas as they do their children? Darwin did so explicitly. Ideas and children both grow older, however, and have to compete in a wider sphere. Few ideas or children develop widespread influence and power, fulfilling parental dreams. Claims of parents about their children's failings are soon viewed as transparent and exculpatory. Perhaps, just as it may be adaptive to overestimate the importance of one's child, treating one's ideas comparably is an essential and evolutionarily derived aspect of the scientific enterprise. This can extend to a group mind-set and the promotion of comparable offspring in selective competition with other groups (Hull 1988c). As scientists, however, we should also develop the ability to recognize quickly and then select against such self-deception before it exceeds acceptable levels of dogmatism and actually impedes progress. I therefore propose as a scientist's first commandment: "*Thou shalt be wary of authoritative leaders promising simple answers to questions about complex phenomena.*"

Ambivalently held group-optimizing predispositions

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Wilson & Sober's (W&S's) explicit and implicit conclusions, for our purposes, are as follows:

1. The innate human behavioral predispositions produced by our biological evolution include group-optimizing ones as well as self-optimizing ones. (We and they focus on the "altruism" facilitating group action, neglecting altruistic acts toward a solitary conspecific.) These predispositions are the result of a mixture of biological group selection as well as individual selection.

2. Where group-optimizing and self-optimizing (including individual inclusive fitness) are in conflict, an innate facultative polymorphism is involved, with situational cues, cultural indoctrination, and other factors determining which disposition will dominate. Humans have an innate group- versus self-ambivalence.

3. The innate group-optimizing predispositions of humans are much less predominant (biological group selection has been more undermined by individual selection) than is the case for the castes of the social insects, where almost complete sterility has eliminated most genetic competition among the cooperators.

4. An older point of view (e.g., Boyd & Richerson 1985; Campbell 1975) that accepted the only-individual-selection dogma for innate human dispositions and saw group-optimizing dispositions as solely the product of cultural evolution is rejected. (This is not to deny the cultural augmentation of innate group-optimizing dispositions.)

If we have paraphrased them accurately (and if they are correct), these propositions have profound implications for psychology and the social sciences. However, their presentation in this brief target article does too little to make biologically evolved group optimization plausible. When W & S come to human examples, they provide only culturally induced dispositions, not biological ones. As presented, the Hutterites are a case of cultural evolution of group optimization. (The strong Hutterite preaching against the innate sin of selfishness supports the position that we believe they reject in point 4 above.) On the other hand, the Hutterites lose some young adults to the larger society each generation. Such loss, however small, is probably selective as to innate personality dispositions. If so, then the culturally evolved organizational inventions and ideology are probably now producing some biological selection of innate group-optimizing tendencies. However, this does not seem to be W & S's point in featuring the Hutterites.

We agree with W & S that "[modern] humans coalesce into cooperative teams at the merest [?] suggestion of a metapopulation structure in which groups can compete against other groups" and that, in general, modern *Homo sapiens* appear to have a "Darwinian algorithm" that predisposes humans for life in functionally organized groups." In addition to noting this general proclivity, however, what we need are detailed plausible scenarios as to how biological group selection took place under the conditions of early human evolution, accompanied by conjectures about the facultative conditions that now trigger the group-optimizing tendencies to override the self-optimizing ones. We also need speculation on the more specific group-selected innate traits involved.

The current human behavior most in need of W & S's explanation may be the volunteer self-sacrificial bravery found occasionally in warfare and in politically motivated terrorism in settings so organizationally chaotic that institutional coercion is not a plausible explanation. The four or more warring factions in Beirut in the 1970s and 1980s provide an ample source of examples. Our present motivational theories, including those of

sociobiology, focused on individual optimization of inclusive fitness, seem inadequate to explain such behavior, however rare it may be. To take another, far removed, example: assuming that Patrick Henry was sincerely willing to act on it, how irrational by all of our motivational theories for him to say, "Give me liberty or give me death," when by "liberty" he meant being ruled and misruled by fellow Virginians rather than by England. It may take biological group selection to explain his willingness to die for that slight difference.

W & S's case for the simultaneous operation of net effective individual and net effective group selection is most plausible where the traits being selected by one level are or were in little or no conflict with those being selected by the other level during the longest stretches of human biological evolution. For voluntary self-sacrificial heroism, however, such as that shown in warfare and politically motivated terrorism, individual selection would seem certain to undermine group selection, leading to no net group selection under most conditions. What seems to be called for is a setting in which loss of membership in one's group was more certainly lethal than the costs of occasional heroism in hunting large animals and in intergroup warfare. Those early human groups must have been tightly bounded, with limited membership, and no individual survival route through joining another group. High rates of biological extinction of whole groups may also be required.

Unnecessary competition requirement makes group selection harder to demonstrate

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Abstract: It is commonly assumed that competition is a theoretically necessary component of any instance of natural selection. This erroneous assumption makes it unnecessarily difficult to authenticate specific cases of group selection. With its elimination, the Gaia hypothesis, for example, becomes theoretically possible.

I welcome the New Group Selection (NCS): anything that genes make can be a vehicle for selection, with one exception – the biosphere itself. I would like to add support to the NCS, and eliminate that exception as well. Biology's long-standing rejection of group selection may have been caused, at least in part, by the mistake of including *competition* as a theoretically necessary component of natural selection. We have assumed, in other words, that natural selection can occur only in the presence of at least two variants of an entity, one of which survives (or reproduces) at the expense of the other. Wilson & Sober (W & S) apparently make that assumption, for example, in dismissing the Gaia hypothesis: "planet-level adaptation would require a process of between-planet selection" (Wilson & Sober 1989, quoted in sect. 2.1). Because it is usually difficult to demonstrate that one group has displaced another, the assumption of competition makes it unnecessarily difficult to authenticate cases of group selection.¹

The following gedanken-experiment demonstrates that competition is not theoretically necessary for selection and thus shows that group selection is consistent with valid evolutionary theory.

The experiment is conducted as follows: a certain number, say 100, of identical "aquatic" environments is set up, each in a sealed container. One hundred identical middle-sized molecules are subjected to a mutagen, and then each is placed in one of the containers. An apparatus makes each of the environments gradually and identically more *hostile*² to the molecules and, one by one, they disintegrate. When only one is still intact, it is removed, cloned 100 times, and again subjected to the mutagen. The environments are standardized and the process is repeated.

After many many iterations, what do we find?

A. The environment is very hostile, compared to the original one.

B. The successful molecule is very robust in that environment, but not robust at all in equally, but differently, hostile environments; that is, it is *adapted* to its environment.

C. This adaptation came about through a process of natural selection.³ Because no variant of the molecule is in a position to displace another variant, this is natural selection *without competition*. (To introduce competition, one would simply throw all 100 molecules into the *same* container on each iteration.)

From these findings, we may conclude that competition is, in fact, not theoretically necessary for selection.⁴ In any given case, therefore, group selection cannot be ruled out solely because competition cannot be demonstrated. A group may acquire adaptive group-level features even if those features do not help it displace another group.

I believe that noncompetitive selection becomes more important as we proceed to higher levels of integration – metapopulation and ecosystem. Indeed, the Gaia hypothesis – that the earth's biosphere as a whole evolved adaptively – rests entirely on noncompetitive selection.⁵

If not competition, what, then, is necessary basis of natural selection? In a recent article (Cloak 1986), I argued that the essential characteristic of natural selection is that an elemental instruction (e.g., a gene or meme) *behaves* (i.e., modifies its environment in some way) and that an outcome of that behavior is an (otherwise nonexistent) *occurrence* of that instruction or its functional equivalent. That process, called *self-emplacement*, can and often does take place via cooperation with other instructions in the construction and operation of individuals, groups, and other vehicles of adaptation.

NOTES

1. Intergroup competition can be claimed, however, even where the unsuccessful group is not extirpated, provided that its potential for reproduction (fission) is reduced, for example, by a reduction in size or a weakening of its internal bonds or a diminishing of its control over resources. By the same token, a successful group, in competition or not, is one that reproduces itself through fission or becomes more likely to do so through increase in membership, and so forth.

2. Making the environment more hostile might encompass increasing or decreasing temperature, pressure, acidity, turbulence, and so on. At later stages, it might encompass making certain resources scarcer, increasing abiotic dangers (windstorms, wildfire, crevasses), making predators faster or fiercer, and so on.

3. What else?

4. In the real world, of course, competition is ubiquitous. It plays the role of the apparatus that gradually turns up the level of environmental hostility, thus accelerating evolution and to a great extent, directing its course.

5. The Gaia hypothesis may still seem difficult to swallow. To us, it is intuitive that Earth's biosphere was either (1) inevitable from the beginning, or (2) resulted from a combination of independent evolutionary adaptation of its component organisms – individuals and (now) groups – and blind luck at various critical points. It is counterintuitive that the biosphere, too, is a product of evolutionary adaptation through natural selection.

Suppose, however, that there are a hundred billion planets in the universe with conditions enough like earth's for evolution to take place. And suppose that the odds are one in a billion that a biosphere including a coterie of sociobiologists will evolve on such a planet. The probability that there are several such biospheres – or at least one – is then fairly high (around 2/3). In that case, we have a natural experiment that parallels our gedanken-experiment remarkably closely. After each iteration, the gedanken-apparatus automatically brings the "world" of the successful molecule to the attention of the experimenter. In the natural experiment, of course, our attention is focussed on the world of a successful biosphere, because it is the only world we can view. We can only surmise the existence of the other planets, successful and unsuccessful, but planet-level selection has taken place, all the same.

Recall that no one is claiming that ecosystem- or biosphere-level selection is paramount. We only claim that it is theoretically possible that such selection has contributed to the shaping of life as we know it; the same claim that is made by W & S for group selection in general. We

are left with the *empirical* question: "Would we be here if some coevolution between most living things on earth were not a reality?"

Group selection's new clothes

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Abstract: The Hutterite example shows not that humans have been group selected but rather the difficulty of getting people to act selflessly. The idea that Hutterites exemplify the human environment of evolutionary adaptedness is not supported by the ethnographic record, in which reproductive equality is rare and meiosis-like rules of group fissioning are nonexistent. We end where we began: group selection is possible but not very likely.

So, we have all been group selectionists all along. This is the message of the theoretical part of Wilson & Sober's (W & S's) article. "Naive" group selectionism of the Wynne-Edwards variety is dead, but those ideas that so successfully displaced it, inclusive fitness theory and evolutionary game theory, are just new, more sophisticated forms of group selection once we think in terms of vehicles. Actually, W & S's discussion of the importance of vehicles is interesting and may have some lasting value. The idea that group selectionism of any variety is going to tell us much about the evolution of human behavior, however, remains doubtful.

W & S choose the Hutterites to demonstrate that group selection has been important in the environments of human evolutionary adaptedness. In fact, the Hutterite example does just the opposite. In the first place, there is nothing very "selfless" about going along with a system that virtually guarantees you several times the reproductive success you could enjoy outside the system. Considering the phenomenal reproductive rates of Hutterites, the real mystery for evolutionary biology is why the rest of us are not trying to join their colonies. Rather than demonstrating that "humans have evolved to willingly engage in selfless behavior whenever it is protected by a social organization that constitutes a group-level vehicle of selection," the Hutterite example merely shows that people have evolved to stick with the social system into which they are born, particularly if it promises such high reproductive success. We do not need to think about "group-level vehicles" to understand this.

W & S are especially fascinated by the ways the Hutterites have found to maintain a communal society despite the countervailing selfish tendencies of human nature. Certainly it is interesting to think about how the Hutterites have been successful, in contrast to so many failed utopian social religious groups (e.g., the Oneidans; see Cronk 1990; Mandelker 1984). W & S may very well be right that a key to Hutterite success has been their invention of mechanisms to keep fitness differentials within the group to a minimum (but see van den Berghe & Peter 1988 for other reasons for Hutterite success). We do not need the notion of group selection for this, however, and the idea may very well make it more rather than less difficult to think clearly about such issues. What the Hutterite example really demonstrates is that it is very, very difficult to get people to act like Hutterites, and most attempts to do so fail miserably. The spirit of cooperation and selflessness W & S identify among the Hutterites is a hothouse flower, and it wilts when exposed to the facts of everyday social existence in run-of-the-mill, unplanned human societies.

This point of view runs very much against W & S's idea that "Hutterite social organization is not unique but represents a fairly common type of social organization in ancestral environments." This view is in no way borne out by the ethnographic record. Certainly it is not true that fitness differentials within groups are typically kept to a minimum in bands and tribes. On

the contrary, the great many recent studies of correlations between cultural and biological success in traditional societies (see Pérusse 1993) have shown that reproductive success is not necessarily equal even in egalitarian societies (see Chagnon 1979). Furthermore, although it may be true that selfless behavior may be encouraged by "a social organization that plays the same functional role as the genetic rules of meiosis" (sect. 2.6.9), there is precious little evidence that such social organizations typified the human environment of evolutionary adaptedness, and certainly they do not typify recently documented band and tribal societies. The meiosis-like rules for colony fissioning among the Hutterites are a fascinating and ingenious contrivance, but that is all they are. I am aware of no other band or tribal society that has anything like such a system. All such societies, as far as I am aware, fission according to genetic relatedness, membership in descent groups, and marriage ties (see Chagnon 1975; 1992 for a classic example). Given that such meiosis-like rules for community fissioning are so rare, it is not surprising that human groups are so much less organism-like than individuals. If a meiosis-like set of rules for group fissioning is indeed a precondition for the evolution of selflessness because of selection on group-level vehicles, then we are back to where we began: group selection is possible but not very likely.

The reason, I think, is that these pioneers and their intellectual heirs have been concerned, not with selection as an end in itself, but with selection as a way of changing gene frequencies. Selection acts in many ways: it can be stabilizing; it can be diversifying; it can be directional; it can be between organelles; it can be between individuals; it can be between groups. Fisher (1930) and Haldane (1932) invoked kin selection as the basis of altruistic behavior and Wright (1988) urged a form of group selection in his shifting balance theory, but the bottom line has always been how much selection changes allele frequencies and, through these, how much it changes phenotypes. This suggests that we should judge the effectiveness of selection at different levels by its effects on gene frequencies.

Much selection goes to maintaining the status quo – eliminating deleterious mutations, removing unfit segregants from superior heterozygotes, or tracking transitory changes in the environment. The bulk of this is surely at the individual level. How about long-term evolutionary progress? If we assume that group fitness is simply the average fitness of its constituents, this can be stated formally as an extension of Fisher's Fundamental Theorem of Natural Selection (Crow 1955). If M is mean fitness, t is time, V_g is the additive genetic variance within a group, and V_m is the total genetic variance among group means, then

$$dM/dt = \bar{V}_g + V_m.$$

If the variance among the means exceeds that within groups, then group selection predominates. Although this formula is given in terms of fitness, it can be modified to reflect allele frequency changes or changes in a trait correlated with fitness. This suggests what to look for and measure. If group properties differ from the individual components, as in the case of altruistic behavior, we can use standard kin-selection theory, or, alternatively, observations on within- and between-group variance (measured by neutral molecular markers) as a way of assessing what potential the population structure offers for the evolution of altruism (Crow & Aoki 1984).

The standard arguments to the effect that individual selection predominates, largely following Fisher (1958), are that the number of individuals is much larger than the number of groups, that variance among group means is usually less than among individuals, and that the time required for proliferation and extinction of groups is long relative to the generation time.

For such reasons, analyses of the evolution of, say, life history patterns are regarded as most convincing when they are formulated in terms of gene frequency change. The lazy man's approach, of which I have been guilty, is to ask what advantage the trait produces. If sexual reproduction is favorable for the group, there is probably an individual selection argument that can be found (not necessarily easily). The justification is that most of the time a trait that is good for the individual is good for the species. If this were not true of a species, if individuals and groups often worked at cross purposes, the species would soon lose out to competitors.

Of course, not all traits are so simple. Behavioral traits, particularly altruism, are most easily understood by group (or kin) selection (but see Simon 1990 for an alternative idea, selection for "docility"). It may well be that of the tens of thousands of human genes, the proportion related to social behavior is a small fraction, but surely a fraction not without interest.

Burying the vehicle

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Wilson & Sober's (W & S's) passion is obviously genuine. I welcome their plainly sincere attempt at clarification and, de-

In praise of replicators

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Abstract: Although selection acts on vehicles, its evolutionary effect is on gene frequencies and, through these, on phenotypes. Hence, equations describing the changes of replicators have understandably dominated evolutionary theory. The effectiveness of selection at a vehicular level is measured by the gene frequency change it produces.

Wilson & Sober (W & S) emphasize the distinction between "vehicles of selection" and "replicators." A vehicle is any entity whose components share more or less the same fate; thus, an individual, a kin group, a trait group, a subpopulation, or a species can be a vehicle. The subunits of a vehicle have the same fitness, for the vehicle has control of them. Thus, it is no accident that some mitochondrial enzymes are coded by nuclear genes; otherwise intracellular mitochondria would compete with each other and the cell would be the loser. Likewise, the organism has dominion over its cells so that they behave cooperatively; when they do not, we have a malignancy. And a population group has (looser) control over its members; if the group becomes extinct, so do all its members. There is a place for research as to the vehicular level at which selection acts.

There are, of course, problems at the borders, as with most classifications. An obvious example is an asexual plant, which is both a vehicle and a replicator. As W & S indicate, vehicles must be identified on a trait-by-trait basis.

W & S also note that group selection has had an undulatory history. There was early naive group selection espoused by such as Alfred Emerson (1942; 1952), employing his loose analogies between termite colonies with their sterile casts and human societies with individualized reproduction. Another was the group-selection advocate, Wynne-Edwards (1962). This led to a backlash of individual- or gene-centered counter arguments, such as the book by Williams (1966). Later, as W & S indicate, there has been a swing the other way.

In contrast, population genetics has undergone no such swings. The emphasis all along, starting with Fisher (1930), Haldane (1932), and Wright (1931) has been on replicators, regardless of the shifting winds of group-selection opinion. Why?

spite myself, I quite enjoy the rhetoric. They are zealots, baffled by the failure of the rest of us to agree with them. I can sympathize: I remain reciprocally baffled by what I still see as the sheer, wanton, head-in-bag perversity of the position that they champion. You see, we really do agree about so much. We come so close to being *like that*. We agree about the fundamental importance of the replicator/vehicle distinction. We agree that genes are replicators and that organisms and groups are not. We agree that the group-selection controversy ought to be a controversy about groups as vehicles, and we could easily agree to differ on the answer. But why, having talked so much sense, do they spoil it all at the bottom line by pretending that their kind of *group-as-vehicle* selection has any illuminating similarity with the kind of group selection that Allee (1943), Emerson (1960), and Co. uncritically misused to explain altruism? They call that kind of group-selectionism naive, which is right, but then they go right ahead and talk of *re-introducing* it. Please do not reintroduce something naive that deserved to be dropped.

We also agree that the individual organism has been oversold on the campus. Far from championing the organism, *The extended phenotype* (Dawkins 1982a) is best seen as an attack on the organism and this should be music to W & S's ears. I coined the "vehicle" not to praise it but to bury it. This is paradoxically, why vehicle is a better name than Hull's "interactor" (Hull 1981). Interactor comes too close to the (messy) truth and therefore does not merit a helpfully decisive burial.

Selection chooses only replicators such as DNA molecules and, conceivably, units of cultural inheritance. Replicators are judged by their phenotypic effects. Phenotypic effects may happen to be bundled, together with the phenotypic effects of other replicators, in vehicles. Those vehicles often turn out to be the objects that we recognise as organisms, but this did not have to be so. It is not part of the definition of a vehicle. There did not have to be any vehicles at all. Darwinism can work on replicators whose phenotypic effects (interactors) are too diffuse, too multi-levelled, too incoherent to deserve the accolade of vehicle. Extended phenotypes can include inanimate artifacts like beaver dams. They can even include phenotypic characteristics manifesting themselves in other individuals and other species. The very existence of discrete vehicles is something that needs an explanation, in the same sense that the existence of sex needs an explanation. No doubt there are good explanations and I essayed three myself in *The extended phenotype*. But the vehicle is not something fundamental, in terms of which other explanations should be framed. You should not feel entitled to ask: "What is *the* vehicle in this situation?"

The cooperative crickets, sculling like Mole and Ratty in unison toward their lily pad, are enchanting. It is deeply unhelpful, however, to claim that the pair is the vehicle of selection. There is no vehicle of selection in this case. It is a terrific vehicle-undermining example. Natural selection favours replicators that prosper in their environment. The environment of a replicator includes the outside world, but it also includes, most importantly, other replicators, other genes in the same organism and in different organisms, and their phenotypic products. Cricket genes for cooperating in the presence of another cooperating cricket prosper. This statement is true and illuminating, in precisely the same sense as the statement that genes for thick, hairy coats prosper in the presence of snow. Like snow, each cricket is part of the environment of the other one's genes.

It would be unfair to accuse W & S of including the snow as part of that which is selected, although it would follow from my view of the world that that is what they are, in effect, doing. But it would be only slightly unfair to offer the following challenge to W & S. Figs depend obligately on fig wasps for pollination, and fig wasps are obligately dependent on fig ovules for food. Each species of fig has its own private species of fig wasp and neither can survive without the other. The underlying game is almost certainly isomorphic with that being played by the two harmo-

nious crickets. W & S should, to be consistent, say that (Fig + Wasp) is the vehicle. Maybe they would. But now suppose that a fig species is equally dependent on a particular species of monkeys to spread its seeds in their dung, and the monkeys are completely dependent on the same figs for their food. Here (Fig + Monkey) is the vehicle. We descend into a criss-crossing, interlocking nightmare of Venn diagrams, but only if we insist on parcelling things up into discrete vehicles in the first place. To push to the *reductio ad absurdum*, are W & S not perilously close to saying of a specialist predator and its uniquely endangered prey, whose shapes and behaviour have been sculpted over many generations by a mutual arms race, that the pair of them constitute a joint vehicle?

Natural selection chooses replicators for their ability to survive in an environment that includes other replicators and their products. Sometimes cooperation among replicators is so strongly favoured that units coherent enough to be called vehicles emerge. But just because a vehicle *may* emerge at a given level, we have no right to assume that it will and I believe the evidence will show that at most levels it usually does not. The question: "What is the vehicle in this situation?" may be no more justified than: "What is the purpose of Mount Everest?" Ask rather: "Is there a vehicle in this situation and, if so, why?"

E pluribus unum?

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Abstract: Wilson and Sober correctly ask whether groups can be like individuals in the harmony and cooperation of their parts, but in their answer, they ignore the importance of the difference between genetically related and unrelated components.

Am I an organism, or a community, or both? I am both – and more – but there is a tremendous difference between the cells that are officially part of my body, and the cells, many of them just as important to my survival, that are not. The cells that compose multicellular me all share an ancestry; they are a single lineage, the "daughter cells" and "granddaughter cells" of the egg and sperm that united to form my zygote. They are host cells; the other cells are visitors, some welcome, some not. The visitors are outsiders because they have descended from different lineages. What difference does this make?

This is extremely easy to lose sight of, especially in contexts in which we treat all these "parties" as intentional systems – as we *should*, but with extreme caution. Unless we are careful, we are apt to miss the fact that there are crucial moments in the careers of these various agents and semi-agents and hemi-semi-demi-agents when opportunities to "decide" arise, and then pass. The cells that compose my bulk have a shared fate, as Wilson & Sober (W & S) rightly stress, but some in a stronger sense than others. The DNA in my finger cells and blood cells is in a genetic cul-de-sac, part of the somatic line, not the germ line. Barring revolutions in cloning techniques (and ignoring the strictly limited, short-lived prospects they have for giving way to replacement cells they help create), these cells are doomed to die "childless," and because this was determined some time ago, there is no longer any pressure, any normal opportunity, no "choice points," at which their intentional trajectories – or the trajectories of their limited progeny – might be adjusted. They are, you might say, *ballistic* intentional systems, whose highest goals and purposes have been fixed once and for all, with no chance of reconsideration or guidance. They are totally committed slaves to the *summum bonum* of the body of which they form a part. They may be exploited or tricked by visitors, but under normal circumstances they cannot rebel on their own. Like the

"Stepford Wives," they have a single *summum bonum* designed right into them, and it is not "look out for number one." On the contrary, they are team players by their very nature.

How, individually, they further this *summum bonum* is also designed right into them (well or ill, but well for the most part, relative to recent circumstances), and in this regard they differ fundamentally from the other cells that are "in the same boat," my symbiont visitors. The benign mutualists, the neutral commensals, and the deleterious parasites that share the vehicle they all together compose – namely, me – each have their own *summum bonum* designed into them to further their own respective lineages. Fortunately, there are conditions under which an *entente cordiale* can be maintained, for they are all in the same boat, and the conditions under which they can do better by not cooperating are limited. *But they do have the choice.* It is an issue for them in a way it is not for the host cells.

Why? What enables – or requires – the host cells to be so committed, while giving the visitor cells a free reign to rebel when the opportunity arises? Neither sort of cell is a thinking, perceiving, rational agent, of course. And neither sort is significantly more cognitive than the other. That is not where the fulcrum of evolutionary game theory is located. Redwood trees are not notably clever either, but they are in conditions of competition that force them to defect, creating what is, from their point of view (!), a tragedy of the commons. The mutual cooperative agreement whereby they would all forego growing tall trunks in the vain attempt to gain more than their fair share of sunlight is evolutionarily unenforceable, to use David Haig's (1993, p. 518) good phrase.

The condition that creates a choice is the mindless "voting" of differential reproduction. It is the opportunity for differential reproduction that lets the lineages of our visitors "change their minds" or "reconsider" the choices they have made, by "exploring" alternative policies. My host cells, however, have been designed once and for all by a single vote at the time my zygote was formed. If, thanks to mutation, dominating or selfish strategies occur to them, they will not flourish (relative to their contemporaries), because there is scant opportunity for differential reproduction. (Cancer can be seen as a selfish – and vehicle-destructive – rebellion made possible by a revision that does permit differential reproduction.) As Skyrms has pointed out (1994; in press; forthcoming) the precondition for normal cooperation in the strongly shared fate of somatic-line cells is analogous to the cooperation Rawls (1971) tried to engineer behind the "veil of ignorance" in his *Theory of justice*. W & S see the parallel between what they call "the genetic rules of meiosis" and social organization, but they draw the wrong conclusion from it, for human social groups are not, in general, composed of near-clones, the way organisms' bodies are (and the way the communities of social insects and naked mole rats are).

Unlike the cells that compose us, we are not on ballistic trajectories; we are guided missiles, capable of altering course at any point, abandoning goals, switching allegiances, forming cabals and then betraying them, and so forth. For us, it is always decision time, and no consideration is alien to us, or a foregone conclusion. For this reason, we are constantly faced with social opportunities and dilemmas of the sort for which game theory provides the playing field and the rules of engagement. Our genes, on the other hand, face these competitive opportunities only under special conditions, in which what Skyrms (1992) calls the "Darwinian Veil of Ignorance" is briefly lifted, such as in cases of "meiotic drive" or "genomic imprinting" (Haig 1992; Haig & Grafen 1991). The "time to be selfish," for genes, is strictly limited, and once the die – or the ballot – is cast, those genes are just along for the ride until the next election.

Skyrms (in press) shows that when the individual elements of a group are closely related (clones or near clones) or are otherwise able to engage in mutual recognition and assortative "mating," the simple game-theoretic model in which defection always dominates does not correctly model the circumstances.

This supports W & S's insistence – long acknowledged but still ill-understood – that there are indeed conditions under which groups can have the "harmony and coordination" required to behave, quite stably, as "organisms" or "individuals" – long enough to permit group-selection effects to occur, for instance. Far from undermining the gene's-eye perspective of Dawkins and Williams, however, this possibility depends on it; it is only from that perspective that the enabling conditions for "group" solidarity can be explained. Or, to put it more provocatively, the conditions under which "nonselfish" coordinations can occur must all be described in terms of how they can be derived, directly or indirectly, from the interactions of "selfish" parts. This does not deny the existence of true group spirit or true selflessness; it just shows that the paths in design space by which it can emerge are narrow and rare. (All the more reason to value it when it does appear, you might say, but it is also worth remembering that the most ubiquitous type of selflessness is the unquestioning bondage of somatic-line cells and organs, exhibiting a xenophobic group loyalty that is hardly an ideal for human emulation.)

Subtle ways of shifting the balance in favor of between-group selection

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Abstract: One factor that makes human behavior particularly interesting in the context of a hierarchical view of selection is that humans are able to shift the balance actively in favor of either between- or within-group selection. Wilson & Sober present some direct ways of facilitating such shifts; I supplement their argument by showing that even more subtle, indirect effects can shift the balance of selection in favor of between-group selection.

There is an old joke about Joe asking his friend Bill for a small favor, to which Bill replies "Why should I do that?" Joe reminds Bill of the time, two years back, when he lent him \$10,000, and the time last year when he pulled him from a burning building. "Yes" says Bill, "but what have you done for me lately?" Supporters and critics of a levels-of-selection approach might look at the first half of Wilson & Sober's (W & S's) target article and ask in a similar vein: "Is this just the same old approach applied to humans, or are there some new, novel predictions stemming from the hierarchical view of selection applied in this context?" The answers to these questions are "sort of" and a resounding "yes," respectively, as W & S's paper, after a rather long review of the group-selection controversy, makes a fundamental contribution to evolutionary biology and evolutionary psychology.

Here, I wish to follow up W & S's remark that, "human behavior not only reflects the balance between levels of selection but it can also alter the balance through the construction of social structures that have the effect of reducing fitness differences within groups, concentrating natural selection (and functional organization) at the group level." W & S discuss reciprocity as one means of changing the balance of within- and between-level selection in favor of the between-level component. As W & S note, however, the Hutterite example clearly shows that mechanisms more elaborate than simple reciprocity exist for shifting the weight of within- and between-group forces. Here, I wish to discuss briefly two such mechanisms – cultural transmission of information within and across groups, and direct observation of the behavior of others.

As we all know from personal experience, you do not necessarily have to be cheated to know that there is a hustler in your area. Two ways to avoid being cheated by people when you first encounter them are: to have observed them cheating on others

beforehand, or to have heard (seen, etc.) information from others that your potential partners are cheaters. One does not need the elaborate and intriguing rules that characterize the Hutterites to develop such behavioral rules. For example, Pollock & Dugatkin (1992) modelled the success of a strategy called Observer TIT FOR TAT (OTFT). A player using OTFT can categorize someone as a cheater if that individual has been seen cheating on others. This strategy, which prevents the user from being "suckered" on initial encounters, is robust under certain conditions. When OTFT succeeds, it is because it incorporates "indirect" information, and uses this information to segregate behaviors and thus change the balance of the within- and between-group selection in favor of the latter. Some experimental evidence exists for the use of this strategy in humans observing others trapped in a prisoner's dilemma (Braver & Barnett 1976).

I have considered how cultural transmission of information (gossip, signs, etc.) about cheaters might effect the evolution of roving cheaters in human societies, that is, con men (Dugatkin 1992). It turns out that some forms of cultural transmission allow the con artist strategy to exist in a population, but only at low equilibrial frequencies, as seems to be the case in humans (Nash 1976). Without cultural transmission, however, the con artist strategy becomes widespread. Cultural transmission of information acts to "inoculate" potential "suckers" and strengthen between-group selection.

These subtler means of detecting cheaters and altering the balance in favor of between-group selection further support W & S's plea for adopting a hierarchical framework when studying the evolution of human behavior.

Some philosophical implications of the rehabilitation of group selection

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The basic argument of Wilson and Sober's (W & S's) target article seems to me absolutely correct. Indeed, as W & S note, in view of the poverty, if not the nonexistence, of the genic selection-based arguments against selection of higher level entities, there is a fascinating historical question to be addressed about the resilience of the prejudice against group selection. Because I find W & S's argument entirely convincing, I shall focus on some philosophical issues that I think need to be addressed in accepting the multilevel picture of selection that they advocate.

No doubt some of the attraction of the idea that a genic perspective eliminates the need to consider higher levels of organization is that it meshes nicely with widely held reductionistic presuppositions. A central ground for such presuppositions is a concern about the possibility of understanding an object that is alleged to have some reality independent of its consisting of some set of real constituent parts. If the reality of the whole implies – as surely W & S's endorsement of the possibility of selective forces acting on higher-level structures does – that wholes enter into causal relations, then a problem arises as to the relations between causal influences acting on the various structural levels contained within the whole. In Sober's (1984) terminology, if there can be selection for properties of groups, properties of the individuals that constitute those groups, and genes within those individuals, consequent on all of these selection processes will be selection of entities at the other levels. And these relations will be quite symmetrical across levels. There seem to be only two possibilities. Either the properties of higher-level structures will be, at least in principle, reducible to properties of lower-level entities, or the on-

logical status of higher-level entities will prove to be on a much more equal footing with that of lower-level entities than is generally supposed even by those who are skeptical about the practical feasibility of reduction.

It is somewhat surprising and disappointing, given that in the past Sober (1984) has so strongly emphasized the causal aspect of selective processes, that there is little discussion of the idea that insisting on the reality of higher-level entities involves attributing some kind of causality to them. Unfortunately, the account of causality to which Sober's earlier work appeals seems to me to be seriously flawed (see Dupré 1993, Chapter 9; Eells & Sober 1983; Sober 1984). More specific to the present purpose, it seems clearly inapplicable to the problems raised by the issue of nested levels within biological systems. The account of causality Sober defended in earlier work starts from the idea that a cause should raise the probability of its effect. Responding to well-known problems about spurious correlations, Sober and others add the qualification that this increase in probability (or at least no decrease) should apply in all sets of background conditions. This condition, however, is most unlikely to be met in the kinds of selective scenarios in which the background conditions include a whole range of features being selected for or against at different levels of organization. (Arguably, it is unlikely to be met at even a single selective level.) Elsewhere I have argued that the most promising solution to such problems is to appeal to a notion of causal powers (Dupré 1993; Dupré & Cartwright 1988; see also Cartwright 1989). This anti-Humean move is highly controversial, but the attribution of causal powers to suitably organized higher-level wholes would, it seems to me, make metaphysical sense of the multilevel picture of selection that W & S so persuasively advocate.

There are further philosophical and biological consequences of the picture W & S present. As I mentioned above, unless one assumes that higher-level properties subject to natural selection are in principle reducible to lower-level properties, the causal efficacy of higher-level properties will require that the higher-level entities possessing such properties be accorded equal ontological status with lower-level entities, a conclusion I am happy to endorse (see Dupré 1993). To make this highly abstract sounding claim more relevant to practical matters, it might be noted that this conclusion renders extremely problematic an idea that continues to occupy something close to the status of a cliché in evolutionary theorizing – the idea that evolution consists of changes in gene frequencies. Why should evolution not be said to consist, rather, of changes in the frequency of properties of whatever objects are the targets of selection? (This would, incidentally, imply a greater unity between processes of natural and of cultural selection.) Beyond this dubious cliché, an adequate philosophical context for taking group selection seriously poses serious problems for major parts of population genetics. If organisms are undergoing numerous selection processes and, at the same time, being selected as parts of larger entities – perhaps several larger entities, including not only groups of various sizes, but possibly symbiotic or parasitic systems as well – the changes in gene frequencies within those organisms may well occur in no systematic way whatever. This appears to conform with a good deal of empirical data; see, for example, the classic study on Australian grasshoppers by Lewontin & White (1960). If this is the case, then the selection coefficients attached to genes in large classes of standard population genetics models will be biologically meaningless. Once again, the only salvation for such models would be a reductionism that insisted that all higher-level selected properties could somehow be traced to a determinate genetic base, something that looks increasingly implausible. Similar conclusions apply, as W & S suggest, to many classes of models in the social sciences that assume methodological individualism.

The general point I want to insist on, therefore, is that if W & S's ontological pluralism about selective levels is to be taken seriously, it raises fundamental problems for a range of

common philosophical assumptions. I suspect that the common predilection for genic selectionism can often be attributed not so much to the bad arguments that W & S expose, as to more or less inchoate assumptions of a more philosophical kind about the ontological primacy of microstructures. I myself have tried to develop in some detail a pluralistic, antireductionistic, philosophical view that provides a metaphysical context entirely congenial to the picture of natural selection that W & S present (Dupré 1993). Whether or not that account is ultimately successful, it seems to me that the story W & S tell indicates a pressing need for some philosophical account of this kind.

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Group selection and “genuine” altruism

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In my book that contains the passages Wilson & Sober (W & S) discuss (Frank 1988), I described a mechanism whereby “genuine” altruism toward nonkin might evolve by natural selection. I argued then, and still believe, that this mechanism rested on selection at the individual level. But W & S have persuaded me not only that it can be viewed equally as group-selectionist in their terms, but also that there is an advantage to doing so. As a committed individual selectionist, I confess that I was *very* reluctant to reach this conclusion. I hope that my attempt to explain my change of heart will caution other individual selectionists against dismissing the W & S argument prematurely.

Mine is an evolutionary game-theoretic model like the ones W & S discuss in their Figure 4. The game is a one-shot, two-person prisoner’s dilemma (PD) played by nonrelatives, and individuals are either cooperators (C) or defectors (D) by genetic predisposition.¹ For this model, as W & S would be quick to agree, the standard individual-selectionist result holds without question: if individual pairings occur at random, defection is the only evolutionarily stable strategy, even though all would do better if everyone were a cooperator.

My point of departure is that cooperation is motivated by emotions such as sympathy and guilt, and that there are observable manifestations of these emotions that enable people to discern them in potential trading partners.² If others’ predispositions could be discovered without cost, cooperators could always pair with one another and avoid interaction with defectors. In that case, cooperators would drive defectors to extinction. More generally, I show that if others’ dispositions are costly to detect, the result is a frequency-dependent equilibrium involving positive shares of both cooperators and defectors.

The feature that differentiates my model from conventional accounts is that pairings between different phenotypes are not random but correlated. To the extent that cooperators can identify one another, the frequency of C-C and D-D pairings will be higher than predicted by the random-pairing model, and it is this feature alone that permits a dominated strategy to be selected at the individual level.

My model involves no group selection in the Wynne-Edwards (1962) sense. Cooperators make headway only if, as individuals, they receive higher payoffs than defectors within each generation. Moreover, selection, viewed in the traditional sense, occurs at the individual level. The complex emotions that support cooperation and the complex means for signaling and detecting these emotions could hardly have been favored if in each generation they entailed a fitness penalty at the individual level.

How does this same story play out in the W & S framework? First, note that the groups to which they refer are not the large,

long-lived groups of the Wynne-Edwards story, but rather the multitude of evanescent pairings in the PD game. Selection pressure can exist within one of these pairs only when the individuals within that pair receive different payoffs – that is, only in C-D pairs. In all such pairs, it favors defectors unambiguously. If cooperators survive, it is only because they experience a higher proportion of C-C pairings than they would if pairings were strictly random. Defectors, in turn, experience a disproportionate share of D-D pairings, which, of course, have lower payoffs than C-C pairings. W & S would identify this *between-group* payoff differential as the force that favors cooperation, and that might thereby compensate for the penalty that cooperation incurs within each group.

W & S have offered a clear and consistent scheme for identifying the locus of relevant selection pressures. The definitions they use are not the same as the ones familiar from the traditional group- versus individual-selection debate. But as W & S make clear, the traditional definitions create troublesome ambiguities that their own do not. More important, by causing us to focus on cases where cooperation involves a within-group penalty, they provide a basis for identifying when cooperation constitutes genuine altruism, rather than merely a behavior that evolves. The alternative is the position taken by Richard Alexander (1992, pp. 184–85), who has said that cooperation in my model cannot *really* be altruism because it involves no fitness penalty at the individual level.

Another advantage of the W & S approach is that, in time, it may help attenuate the doctrinaire character of the traditional debate between individual and group selectionists. As W & S note, the rigid terms of this debate often push people into extreme positions – as in the case of individual selectionists who were reluctant to concede that selection occurs at the group level even in the case of eusocial insects. Once we recognize that group membership is often fleeting, that individuals typically belong to many different groups at once, and that groups often do not consist of individuals chosen at random, many new and interesting selection possibilities emerge. I suspect that most of these will prove consistent with the traditional individual-selectionist vocabulary. For example, in each of the four payoff matrices shown in W & S’s Figure 4, the only behaviors that evolve are those that would have been freely chosen by a fully informed individual concerned only with maximizing his fitness. But perhaps there will also be a few surprises. If so, they seem much more likely to come to light under the W & S framework than under the traditional one.

That said, I must add that the Hutterite example is a curious choice for illustrating the value of the new group-selectionist perspective. As many individual selectionists have emphasized, constitutions, laws, moral norms, and other elements of human culture are intelligible as means of resolving social dilemmas. In close-knit groups like the Hutterites, it is relatively inexpensive to punish individuals who pursue interests that harm others unduly. I do not doubt that social conditioning has induced many Hutterites to put their group’s interests ahead of their own, even absent any threat of punishment. Yet it is hard to imagine a society in which transgressions would be less likely to go unpunished. The example thus seems almost to beg skeptics to respond that individual Hutterites are merely being prudent by following the rules.

Fortunately, there are many compelling examples of other-regarding behavior familiar in our own culture. For example, most diners leave tips even in out-of-town restaurants they never expect to visit again. And many people drive 30 minutes through traffic to dispose of unwanted pesticides properly rather than simply pour them down their basement drains. In these cases, the probability of being detected and punished for doing the wrong thing is too low to constitute a plausible motive. Genuine altruism is at work here, and it is by no means uncommon. If people with altruistic predispositions are observably different from others, altruists can interact selectively with

one another and thereby reap the fruits of cooperation. Viewed in this fashion, altruism is a strategy that can be reproductively advantageous to the individuals who follow it. Equivalently, and as Wilson & Sober would have it, the selective pressures favoring altruism are concentrated at the group level, where groups are defined as the relevant interacting pairs. Both perspectives permit us to say that genuinely altruistic behavior can be favored by the forces of natural selection.

NOTES

1. Figure 4B in W & S is an example.
2. Can we detect cooperative dispositions in others? Gilovich, Regan, and I have recently (1993) published the results of experiments in which subjects of only brief acquaintance were able to make remarkably accurate predictions about who would cooperate in a one-shot PD played for money. It seems plausible that people of long acquaintance would be able to make still more accurate predictions.

Me, you, and us: Distinguishing "egoism," "altruism," and "groupism"

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Abstract: Attention is drawn to significant distinctions implicit in our everyday nontechnical conceptual scheme. Three forms of motivation are distinguished: "egoism," "altruism," and "groupism." The relationship between them is considered. It is argued that groupish motives (as defined here) are not of themselves either altruistic or selfish ones in the relevant senses.

To the "embattled minority" in the human sciences who face "a monolithic individualistic world view" (sect. 2.4) among their peers according to Wilson & Sober (W & S), one might add a similar minority of philosophers, of whom I am one. As I argued in a previous *BBS* commentary (Gilbert 1989b), the conceptual scheme embodied in everyday thought and talk allies with the embattled minority, at least with respect to some ways of construing "individualistic."

In a number of places (for instance sect. 2.3, Note 21) W & S suggest, congenially, that the categories and distinctions made in everyday thought are quite relevant to the concerns of evolutionary biologists. There are some significant distinctions implicit in our everyday conceptual scheme that came to mind at various points in my reading of their interesting target article.

Consider the following fragment from W & S: "The external social conventions that make freeloading difficult . . . must be supplemented by a psychological attitude of genuine concern for others; a direct calculus of group-interest rather than self-interest is essential" (sect. 2.6). It would be quite natural to interpret this as alluding to three different forms of motivation, forms relating to others, one's group, and oneself, rather than two (as the phrasing may suggest). In any case, it is important to distinguish the three forms in question and to consider the relationship among them.

Because of space limitations what I say will necessarily be quite rough. I draw on investigations published in Gilbert (1989a; 1990) and elsewhere. (These focus on everyday collectivity concepts such as the concept of a social group, a group's goal, etc.)

With the important caution that these terms are being defined anew here with no deference intended to any established technical uses, the three forms of motivation in question will be labeled "egoism" (or "selfishness"), "altruism," and "groupism." ("Groupish" is W & S's nice term.)

One acts from *egoistic* or *selfish* motives when acting to promote *one's own* goals, needs, and so on. Thus, I act egoistically if I prepare a meal to satisfy my own hunger. One acts

from *altruistic* motives when promoting another person or thing's goals, needs, and so on. Thus, I act altruistically if I prepare a meal at a soup kitchen so that certain others who will arrive there should be fed. Last, one acts from *groupish* motives when one acts so as to promote what one perceives as "our" goals, needs, and so on. Thus, I act groupishly if I prepare a meal at 6:00 because we plan to get to the play at 8:00.

What is the relationship among these categories? First, motives of all three types can be present at once. I might prepare a meal at 6:00 because (a) we plan to get to the play at 8:00, and (b) I am very hungry, and (c) I know that you are very hungry, too. Second, if present together, motives of these different types need not be in conflict: they need not necessarily push in different directions. This is clear from the above example.

Is it possible to act from each of these types of motives alone, without the necessary inclusion of a motive of the other kind? Intuitively speaking, one can act to promote one's own goals without also acting to promote anyone else's, and without any groupish intentions. Again, it seems that one can act altruistically without either selfish or groupish motives. Finally, it seems that one can act groupishly without either selfish or altruistic motives. This is perhaps the hardest point to allow, and the most relevant here, so I will focus on it.

Though the main issue is the independence of groupism from altruism, it will be useful to start by questioning whether people can act groupishly without also acting from selfish motives. On the face of it, they can. Consider what might run through Jack's mind just before he runs into the kitchen at 6:00: "Oh my goodness, we are going to the play at 8:00! If someone doesn't get dinner now, we'll never be ready! No one else will be here till 6:15, so I'd better get dinner." Here there is no explicit reference to what Jack himself wants or needs, no reference to his own hunger, for instance, or his own desire to see the play.

But wait a minute, someone may say. What is it, after all, for us to have the plan of going to the theater at 8:00? Is it not for me to have that plan, and for you to have that plan, perhaps with some additional conditions such as common knowledge of the plan? (cf. Bratman 1993.) As I understand our everyday conceptual scheme, the answer is No. For us to have a plan is for us to be jointly committed to uphold that plan as a body. A joint commitment is a commitment that is seen precisely as joint. (For a careful account of the meaning of "joint commitment," a technical term, see Gilbert 1993a, pp. 692–95; see also Gilbert 1993b.) I have argued at length and in a number of places that something like this analysis of "our plan" holds for a whole range of concepts including "our goal" and "our belief" (on the latter see Gilbert 1987; 1989a; 1994).

Clearly, if I have a contrary plan of my own, there will be conflict within me. That is, there will be conflict between our plan and my own. And this could happen. Our plan may be to go to the theater at 8:00, but my plan may be to sabotage our plan, and have an early night instead. Perhaps I intend to fake a terrible headache. But if we have a plan, must I not also have the corresponding plan myself (whatever precisely the corresponding personal plan would amount to)? Not necessarily. If we have a plan, and neither of us has any contrary personal plan, then there is already enough in the situation to motivate us (because joint commitment is motivating). So no corresponding personal plans are necessary. They are, it would seem, perfectly possible, but they need not be present.

What, next, of groupish motives vis-à-vis altruistic motives? If I prepare dinner on account of a plan *we* have, must I be acting for the sake of some plan of *yours*? Intuitively the answer here will be the same, *mutatis mutandis*, as it was with respect to my own personal plans. Acting groupishly, I do not act for the sake of some plan of yours, that is some plan of *your own*, or, as we might put it rather quaintly, some plan that *you own*. Rather, I act for the sake of a plan of *ours*: a plan that we own jointly.

When I act for the sake of *our* plan, or in the light of *our* plan, my concern, then, is not with myself considered in isolation

from the group we help to constitute, nor with you so considered. In particular, my concern is for you only insofar as you are bound up into a "we" with me, by virtue of our having a plan. My concern therefore would not seem to be appropriately described as involving a "genuine concern for others."

A point to stress, then, is that to bring in groupish motives is not to bring in altruism, any more than it is to rule out egoism. It is to bring in something that transcends *both* altruism *and* egoism, at least as I have defined these here.

One can, of course, define altruism differently, and such an alternative definition may well be appropriate and fine for other purposes. However one defines particular terms, one should be careful not to cloud over some distinctions that are (a) made within our everyday conceptual scheme and (b) operative in our practical reasoning, that is, the reasoning that goes on when we deliberate about what to do in the course of daily life.

Contextual analysis and group selection

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Abstract: Contextual analysis is a method for statistically analyzing selection acting at multiple levels in natural populations. In addition to being a statistical procedure, it provides a conceptual shift in our understanding of selection: it becomes apparent that the mathematical equivalent of group selection is much more common than previously believed.

One of the important recent advances in the study of group selection is the development of contextual analysis (Goodnight et al. 1992; Heisler & Damuth 1987). On the surface, this method is simply a statistical tool for analyzing selection acting on multiple levels, but it is also a major shift in the manner in which selection is understood.

Contextual analysis is an extension of the analysis of phenotypic selection advocated by Arnold and Wade (1984a; 1984b; see also Crespi & Bookstein 1989). In these analyses, selection and the response to selection are logically separated. An analysis is then done on the ecological factors that influence fitness, without regard to whether there will be any response to this selection. This separation of selection and the response to selection, although perhaps surprising to many, follows logically from the field of quantitative genetics. Quantitative genetics makes a clear distinction between selection, which is the change in the mean of a trait within generations, and the response to selection, which is the change in the mean of a trait between generations. Contextual analysis extends this approach by including not only traits measured on the individual, but also "contextual" traits measured on the groups to which they belong. Together, these are used in a multiple regression analysis of relative fitness on the individual level traits, the group means of the traits, and the contextual traits. If there is a significant partial regression of relative fitness on the group mean of an individual trait or a contextual trait, we say that group selection is occurring. Theoretical analysis indicates that contextual analysis can be used successfully to analyze classic models of group selection, individual selection, and simultaneously acting group and individual selection (Goodnight et al. 1992).

Although the above description outlines the statistical aspects of contextual analysis, it does not do justice to the philosophical implications of this statistical approach. First, it is important to point out that contextual analysis is basically the statistical equivalent of the approach that Wilson & Sober (W & S) advocate. They suggest that we pose questions such as: "Do genes within a single individual share the same fitness?" In contextual analysis all members of the same group have the same value of a

contextual trait. A significant regression of relative fitness on this trait indicates that all members of the same group share (at least to some extent) the same fitness. It is more general than the W & S approach, because when selection is acting simultaneously at two levels, say, the group and individual level, the fitnesses of the individuals within a group will not be the same (because of individual selection) even though they share a common fate to some extent (the result of group selection).

Contextual analysis makes it clear that within a system of analysis, fitness can be assigned at only one level (be it gene, organism, or group). Moreover, fitnesses are assigned at this level for all traits, both individual and contextual. In most situations, fitnesses will be assigned at the level of the organism; however, Damuth and Heisler (1988) point out that this is not a logical necessity. Because it is central to contextual analysis, I prefer to use the term "individual" for the level at which fitness is assigned and "organism" for an individual metazoan.

The question becomes: How can group selection be detected when fitnesses are assigned only at the level of the organism? When there is a partial regression of fitness on a contextual trait, then there is group selection. As an example, imagine that there is only group selection acting. In this case, even though fitnesses are assigned at the level of the organism, all organisms within a group will have identical fitnesses. There will be no partial regression of relative fitness on the individual traits, but there will be a partial regression of relative fitness on the contextual traits.

A second point is that I refer to "the level at which fitness is assigned." This is because in contextual analysis the level at which fitness is assigned is a decision made by the investigator. All changes at and above the level at which fitness is assigned can be studied as selection; all changes below that level must be studied as "development" or its equivalent (Damuth & Heisler 1988). Thus, in the contextual view, an "individual" is simply the lowest level of organization the investigator chooses to recognize. We normally assign fitnesses at the level of the organism; thus, changes below the level of the organism are typically viewed as developmental changes. However, in studies of meiotic drive, for example, it might be appropriate to assign fitnesses at the level of the gene.

What becomes clear from contextual analysis is that many forms of frequency-dependent selection, density-dependent selection, and kin selection that occur in structured populations are the mathematical equivalent of simultaneously acting group and individual selection. The main conclusion, then, is that the mathematical equivalent of group selection is exceedingly common in nature. Yet, although common, it rarely takes on the clear form of selection acting among equivalent genetically isolated entities that most people consider when discussing group selection (e.g., Maynard Smith 1976). Using contextual analysis we are likely to identify group selection more frequently when it is occurring. Perhaps in this way we can then truly understand its role in evolution.

Putting the cart back behind the horse: Group selection does not require that groups be "organisms"

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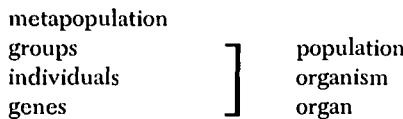
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Abstract: Wilson & Sober misrepresent the group selection debate: the debate concerns whether groups are vehicles (or interactors), not whether groups are "organisms."

In Wilson & Sober's (W & S's) view, an "organism" is "any biological entity whose parts have evolved to function in a

harmonious and coordinated fashion" (Note 1). By contrast, an "individual" is "a single flesh and blood creature" such as a bird (Note 1). Thus, in their terminology, individuals are a subset of the class of organisms: individuals are perhaps the most common sort of organism, but other biological entities (including insect colonies and groups of individuals) can be organisms if they display the right kind of functional organization. Although these definitions are nonstandard, they will be adopted for the purposes of this short commentary.

According to W & S, the central question in the group-selection debate is whether groups can be *organisms*. This is clear when W & S assert that the central question in the debate over group selection is whether groups can be "like *individuals* in the harmony and coordination of their parts" (last paragraph of sect. 1.3). This claim is also built into their "frameshift" model. In their view, selection processes require three different kinds of entities: organs, organisms, and populations. This tripartite "frame" can be viewed as sliding along the fixed biological hierarchy shown in the left column.



In the standard case of natural selection, groups play the role of the population, individuals play the role of organisms, and genes play the role of organs, but we can also frameshift up so that groups play the role of organisms. The implication is that group selection can occur only if groups are functioning as organisms (i.e., if they are functionally organized). Although this may appear to be a trivial or innocuous claim, I believe this is a misleading way to frame the debate.

Here's the problem: In stating that the central issue concerns whether groups are "organisms" (functionally organized), W & S suggest that such functional organization is a *necessary prerequisite* for group selection. This is simply not the case, however. Groups can function as units of selection, that is, vehicles or interactors (for the purposes of this commentary I assume that these concepts are identical) just so long as the individuals within the groups share a common fate.¹ Consider W & S's example of the leaf-riding crickets (sect. 1.6). When the crickets began sharing leaves, their actions were poorly coordinated; the temporary groups did not function as "organisms" because the individual crickets did not work well together. The coordination of their actions, then, is one possible *product* of (not a *prerequisite* for) group selection. Furthermore, if group selection is opposed by strong individual selection, close coordination between the crickets may not evolve, *even though group selection is occurring*. Depending on the precise benefits of cooperation and the strategies available in the population, individual selection favoring selfishness can prevent the development of cooperation, even when group selection favors cooperation. Thus, the process of group selection neither requires nor guarantees that groups be "organisms." We need to retain the proper relation between selection and functional organization: natural selection is the driving force (the horse) and functional organization (the cart) is one possible result of selection at that level.

This is an important point, because if we recognize that group selection does not require functional organization (either as a necessary prerequisite or a necessary consequence), then the failure to find such organization is not definitive evidence against group selection.

This criticism of the way W & S present the group selection debate should not obscure our agreement on more significant issues. Once we recognize that evolutionarily stable strategies and kin selection models are *not* alternatives to group selection, we must recognize that group selection is a significant force in evolution. This means that we need an explicitly hierarchical

theory of evolution. Furthermore, if group selection is a significant force and humans evolved in small groups, then we must recognize the possibility that group selection can be invoked to explain some aspects of human social behavior. Wilson & Sober have built an impressive case for their claim that group selection models have a legitimate role to play in the social sciences.

NOTE

1. In Note 9, W & S seem to recognize that the process of group selection does *not* require that groups be organisms, but as I have shown, many other aspects of the paper misleadingly suggest that group selection requires group-level organisms.

Replicators and vehicles? Or developmental systems?

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Abstract: We endorse Wilson & Sober's conclusion that whether groups are replicators is irrelevant to whether they are vehicles of selection. However, we would urge them to reject the replicator/vehicle distinction, which requires an implicit nature/nurture dichotomy. The alternative "developmental systems" perspective is better able to describe the role of culture in the evolution of group-level adaptations.

Wilson & Sober's (W & S's) treatment of the group-selection question is impressively clear and simple. We endorse their conclusion that whether groups are replicators is irrelevant to whether they are vehicles of selection. We would urge them to go further, however, and reject the replicator/vehicle distinction.

W & S have shown that the argument which moves from the view that genes are the sole replicators to the conclusion that they are the sole or main units of selection is a non sequitur. The argument for the original view, that genes are the sole replicators, is little better. Dawkins (1982a, p. 99) argues that "The special status of genetic factors is deserved for one reason only: genetic factors replicate themselves, blemishes and all, but non-genetic factors do not." But what exactly is it that has the power to replicate itself? A segment of DNA isolated from the cytoplasmic machinery of ribosomes and proteins has no such power. Suppose we enumerate the whole cellular machinery needed to copy a strand of DNA, including the independently inherited centrioles, mitochondria, and so on. This is very far from Dawkins's original vision. Yet under natural conditions even this system only replicates itself because of the presence of many other resources. Parents do not, typically, toss the zygote naked into the world. They place it in, and often guide it through, a highly structured developmental environment. The organism quite literally *inherits* the elements of this environment. Previous generations reproduce these elements as part of the process of reproducing the causal conditions that gave rise to themselves. In humans, for example, the development of language requires exposure to a speech stream just as surely as it requires a human genome. In this sort of way, previous generations provide an enormous range of developmental resources in addition to the genes. Developmental systems theory draws attention to these massive, uncontroversial, but somehow utterly overlooked forms of extragenomic inheritance (Gray 1992).

The full range of developmental resources that are required to reconstruct the life cycle of a particular lineage constitute the "developmental system" of that lineage. Genes do not replicate themselves. They are part of the developmental system of a developmental process (life cycle) which replicates itself. (Gray 1992; Griffiths & Gray 1994; Oyama 1985).

Defenders of the replicator concept have always admitted when pressed that genes only replicate themselves in a develop-

mental context. They have made their real stand on the asymmetry between those inherited factors that contain information – the genetic blueprint or program – and those that provide mere physical materials. Only the latter are true replicators. No such asymmetry exists, however, as has been made clear by authors such as Susan Oyama (1985; 1989) and Timothy Johnston (1987). An event carries information about another event to the extent that it is correlated with that other event. The “transmission” of information is a matter of the systematic dependence of one system on another. There is a systematic dependence between an organism’s phenotype and its genetic inheritance, but there are systematic dependencies of the same sort between the phenotype and many other developmental resources. Changes in these resources are reflected in changes in the phenotype, so they, too, must be transmitting information to the phenotype.

This symmetry between different causal factors in development is intrinsic to the mathematical concept of information. In the traditional picture of the development of an “innate” trait, the nongenetic developmental factors constitute the channel conditions under which the organism carries information about its genes, whereas in the traditional picture of “learning,” the intrinsic organization of the organism constitutes channel conditions under which the state of the organism carries information about environmental factors. It is always possible, however, to reverse the roles of the sender and channel conditions. We can interpret the development of the “innate” trait as a case in which the genes constitute channel conditions under which the organism carries information about some nongenetic developmental factor. We can also interpret the learning case as one in which the environmental factors are channel conditions under which the state of the organism tells us about its genes.

The developmental-system, or constructionist, approach does not distinguish a single component of the developmental system as the “signal” or source of information. Even the idea that the information reflected in the organism’s development is contained in the whole set of developmental resources fails to do justice to the fact that the resources that construct later stages of the developmental process are constructed by earlier stages. Developmental information, as Susan Oyama (1985) has argued, is itself the product of an ontogeny.

A developmental-systems approach to replication is entirely consistent with W & S’s hierarchical conception of the evolutionary process. Life cycles, and the developmental systems associated with them, can be nested within one another in just the same way as “vehicles.” The life cycle of an individual ant is nested within the life cycle of the colony. Like the life cycle of an individual, that of a colony is reconstructed by the interaction of a range of inherited resources.

The developmental-systems approach may offer a better way of conceiving the role of culture in the evolution of group-level adaptations in humans. Culture is likely to be a key developmental resource for humans. Many species-typical features of human psychology may depend on stably replicated features of human culture. Many psychological features which are specific to particular human cultures may nevertheless have evolutionary explanations, because this variation may reflect differentiation amongst lineages of developmental systems. These ideas concern the developmental systems of individual people. But if human groups have been subject to selection and have group-level adaptations, then groups may have their own developmental systems, which explain the maintenance of group characters across “generations.” Rather than seeing cultures which encourage altruism as expressions of “Darwinian algorithms” evolved in the Pleistocene and genetically programmed into each individual (Cosmides & Tooby 1987), one can see them as developmental resources passed on by groups in that culture. These resources help to reconstruct the relevant group adaptations in the next generation of groups.

An interesting example of a group developmental system is

found in the fire ant *solenopsis invicta* (Keller & Ross 1993). Colonies with single queens differ markedly from those with multiple queens. Queens from the two types of colony also differ. These differences are thought to help in the construction of colonies of one type rather than the other. The differences between queens are induced by the type of colony in which they have been raised, as shown by cross-fostering experiments. Exposure to the pheromonal “culture” of one type of colony produces an individual which is a developmental resource for the construction of colonies of that type.

By analogy with this example, the ability of human groups to replicate their group adaptations may depend not on “genes for culture,” but on the extragenetic inheritance of cultural resources.

Reconstructing the real unit of selection

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Abstract: In contrast to the many attempts to solve the problem of selection levels on the basis of the paradigmatic replicator/vehicle dichotomy, it is possible to reintroduce the physical concept of the “living system” as a fruitful alternative to both reductionist and holistic approaches.

The basic dilemma concerning the “unit of selection” is associated with the fact that it is exactly the concept of such a unit that has been definitively destroyed through the many controversies about the real mechanism of evolution. In this respect, Wilson & Sober (W & S) hit the mark with their remark that “the term ‘unit of selection’ has become ambiguous because it refers to both replicators and vehicles, depending on the author.” On the one hand, we have evolutionary geneticists who, inspired by fantastic discoveries in molecular biology, were very successful in their attempt to reduce almost the entire process of evolution to purely quantitative shifts in the frequencies of specific kinds of molecular replicators. On the other hand, we see scientists not so impressed by the dominant genetic paradigm who have tried to save their field of investigation by separating as much as possible of the rest of biological phenomena (i.e., the majority of phenotypic traits) from the direct influence of genes. Both approaches, if applied exclusively to explain the phenomenon called “evolution,” are basically wrong because in both cases, something is lacking that really would permit us to speak of an autonomous entity underlying and constituting the evolutionary process. Thus, it is quite obvious that replicators need phenotypic “vehicles” (Dawkins 1976) to be transported. At the same time, however, it is also clear that such vehicles will never move or even behave in an adaptive manner if not set in motion and controlled by “intelligent” drivers, that is mechanisms of any kind provided with the relevant information, or, in more pragmatic terms, the specific knowledge to handle biological “machines” such as cells and bodies.

The question now concerns whether it is really necessary to reconstruct the unity of a truly universal biological unit to find the correct answer to the selection-level problem. W & S, in emphasizing the impact of potential higher categories of vehicles (mainly groups), obviously think it unnecessary, as they try only to extend the problematic dichotomy between replicator and interactor (Hull 1980). In such a perspective, complex vehicles can easily be founded on rather arbitrary grounds; one simply declares that “groups (and populations and cultures and civilizations) are real.” However, to accept the existence of real competition between groups the idea of the group as a true unit must already be presupposed. Hence, as in the extreme reduc-

tionist paradigm ("only genes are real"), this argument cannot avoid becoming circular.

In my opinion, the outlines of a basic unit in both the primordial biological ("organism," etc.) and the selectionist sense (frequency of replication) can best be discerned if special attention is paid to the concrete interdependencies between the potential candidates for a general unification. For this purpose, let us consider the very illustrative example of the defense of a village by its inhabitants (who build a stockade, fight together against an aggressor, etc.). If one proceeds step by step to assess the major causal relationships, the result can be described as follows:

1. Any gene involved depends 100% on the fate of the chromosome carrying it.
2. Any chromosome involved depends 100% on the fate of the genome carrying it.
3. Any genome involved depends 100% on the fate of the cell carrying it.
4. Any cell involved depends 100% on the fate of the multicellular body carrying it.
5. Any individual involved can depend indirectly, but must not depend 100%, on the fate of the group "carrying" it. In other words: the welfare/death of an individual is not absolutely associated with the welfare/death of the group, because – in sharp contrast to genes, chromosomes, genomes, and cells – it can never be excluded with certainty that a single individual survives.

This result, which is nothing but the logical consequence of a physical rather than just a metaphorical interpretation of the shared fate-concept of selection (cf. the motto "we're all in the same boat"), seems trivial, but its implications are not. They indicate that the crucial unit is to be found in the term "system" in its concrete material sense. If there exists only a small spatiotemporal break in coherent determination between different elements of a supposed entity, we should be cautious about calling it a unit, because selection will always have the possibility of treating them separately. This, however, does not preclude quite different phenomena, ranging from "naked" viruses to "well-enveloped" multicellular organisms, from being true systems in an evolutionary sense, given stable causal coherence among its constituents. For the special case of a group of human individuals, we must postulate a far greater "closeness" and interdependence than actually exists to call it a real system that undergoes evolution by natural selection. Of course, it is still possible that one day this might happen, but – as impressively documented by Buss (1987) – the evolution of the existing units of selection (self-replicating molecules, complexes of molecules, isolated cells, aggregates of cells) already had to solve a variety of quite severe organizational problems to finally achieve, after many millions of years of mutative experiments, the highest level of multicellular individuality.

Empirically equivalent theories

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Abstract: Wilson & Sober have shown how to reinterpret individual selection theories as trait-group selection theories. However, Dugatkin and Reeve (1993) have shown how to translate back and forth between trait-group and broad-based individual selection theories. So, trait-group selection theory can in turn be reinterpreted as a broad-based individual selection theory. Paradoxically, these theories are literally incompatible and yet observationally equivalent.

Wilson & Sober (W & S) argue that "what seem to be competing theories, such as kin selection and reciprocity, reappear as

special cases of group selection." Is "trait-group" selection in fact group selection? I shall pursue the objection that W & S's "group selection" is only a redescription of individual selection.

If "trait-group selection" is just a disguised form of individual selection, two results emerge. First, we should feel free to use it in explaining behavior because the old prejudices and arguments against group selection do not apply. There is no need to "reintroduce" group selection. Second, it is no surprise that individual selection theories are cases of a trait-group selection, that is, individual selection. What had seemed a controversial thesis reduces to a logical truism.

We need to confront the basic conceptual question, Are group and individual selection distinguishable? My answer is paradoxical: trait-group selection and broad-based individual selection are literally incompatible, yet observationally equivalent theories. This answer challenges realism by asserting that we have several equally empirically validated theories of reality, not one. We describe reality relative to one theory or another, but there is no unified account beyond noting that the two mechanisms have the same observable evolutionary effects.

Following Putnam (1992, p. 38–39), theories T1 and T2 are literally incompatible and yet equivalent calculative devices if and only if conditions (A), (B), (C), and (D) hold:

(A) T1 and T2 cannot both be true when interpreted literally. According to W & S's literal interpretation, a case of selection may be a case in which only the individual is the vehicle (the standard individual selection view) or one in which both individuals and groups are vehicles (the hierarchical view in which trait-group selection is cast). Logically, the individual selection view and the hierarchical view cannot both be true. On W & S's causal analysis of the units of selection, the individual selection theory and the trait-group selection theory differ in their causal accounts of selection. Where individual selectionists see only fitness variations between individuals, with group-structure affecting individual fitnesses, hierarchic selectionists see fitness variations between both individuals and groups. Individual selection theory and trait-group selection theory do posit alternative mechanisms, and so are literally incompatible theories.

(B) T1 and T2 share a common mathematics. Many studies have shown that the mathematics of gene, individual, kind, and trait-group selection approaches are closely related or equivalent. Some have shown that efforts to find a crucial experiment cannot succeed because the closely related mathematics given equivalent observational consequences (Grafen 1984; Queller 1992a; 1992b; Ratnieks & Reeve 1991).

(C) T1 and T2 are mutually, relatively interpretable, that is, there are definitions of the terms of T2 in the language of T1 and of T1 in T2, such that if we "translate" the sentences of T1 into T2, then all the theorems of T1 become theorems of T2 and vice versa. "For broad-sense individual selectionists, 'individual selection' refers to evolution resulting from the higher population-wide average fitness of individuals bearing some trait; for the new group-selectionists, 'individual selection' more narrowly refers to selection only within groups" (Wilson 1983a; Wilson & Sober 1989). Thus, the new group selectionists have simply partitioned the individual selectionist's concept of individual selection into two components, only one of which is called "individual selection" (Dugatkin & Reeve 1993). Here are the essential translation procedures:

In passing from an individual-selectionist to a trait-group selectionist view, we (i) draw imaginary boundaries around collections of interacting individuals, thus forming groups . . . , (ii) describe how the behavior of interest affects the reproductive output of an individual within the group relative to other members of the group, and (iii) describe how the behavior affects the reproductive output of the group as a whole. . . . The reverse translation also is simple: Take an individual's fitness within the group (e.g., its proportionate offspring representation), multiply this relative fitness by the group's overall absolute output and sum across groups. (Dugatkin & Reeve 1993)

(D) The translation of each into the other preserves the

relation of explanation and exactly the same phenomena are explained by both. For example, why are Hutterites so selfless? According to the trait-group explanation: because group members' aid to their sect is disfavored by within-group selection but is more strongly favored by between-group selection. According to the broad-based individual explanation: because group members' aid to their sect enhances their inclusive fitnesses (the Hutterite threat to cut off and exclude selfish cheaters makes psychological selflessness more beneficial to individuals than psychological selfishness). Using the translation manual above, we can move back and forth between these incompatible mechanisms to explain exactly the same phenomena. Broad-based individual selection theory and trait-group selection theory give exactly the same empirical predictions about whether a gene (or trait) will increase, decrease, or stay the same in frequency in the population for n generations. Thus, any group-benefiting adaptations posited by the new group selection theories can be understood in terms of broad-based individual selection theories.

Groups as vehicles and replicators: The problem of group-level adaptation

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Evolutionary biologists have consistently applied the term "adaptation" only to traits that arose through a process of natural selection (Brandon 1978; 1990; Gould & Vrba 1982; Lewontin 1978; Sober 1984; Williams 1966; 1993). Such a process requires not only that there be individual differences in characteristics that are causally related to differences in reproduction and survival, but also that these differences be transmissible from parents to offspring. As Sober (1984, p. 151) put it: "Selection implies evolution only when no evolutionary force counteracts it and the trait being selected is heritable" (italics in the original). Wilson & Sober (W & S) build a convincing case that groups can be a *vehicle* of selection, but they largely ignore the processes that might allow groups to function as *replicators* (Dawkins 1976; Hull 1980).

Although W & S never explicitly discuss this neglect, the justification for it is implicit in their discussion of the adaptationist program. They argue that "one of the virtues of the adaptationist program is that it can be used with minimal knowledge of the physiological, biochemical, and genetic processes that make up the organisms under examination" (sect. 1.1). It appears to require little more than an understanding of which features of organisms are beneficial and which are not. In fact, it also requires that organisms have characteristics that allow their traits, beneficial or not, to be passed to their offspring. It requires that offspring resemble their parents, for only then can a trait arise through a process of natural selection.

For individual organisms, this requirement poses no problem. Long before Mendel's work and its discovery, the everyday experience of human beings confirmed it as an empirical fact. Animal breeders have known for centuries that sheep with fine wool can be produced more easily by breeding parents with fine wool than by breeding parents with ordinary wool, to cite only one example. The very familiarity of this fact makes it easy to overlook, and the adaptationist program proceeds without a detailed understanding of genetics because it requires nothing more than this resemblance between parents and their offspring. Inheritance of group-level characteristics poses more of a problem. The apparent lack of a mechanism for inheritance for group-level characteristics is the primary reason gene selectionists have denied that groups can be units of replicator selection (Cronin 1991; Dawkins 1976; Williams 1966). Thus, W & S

neglect a critical question: Are there mechanisms that produce resemblance among groups analogous to the resemblance between parents and their offspring? Only if the answer is yes can evolution by natural selection at the group level occur, producing group-level adaptations. Reviewing W & S's explication of inclusive fitness theory (sect. 1.5) reveals examples both of such a mechanism and of why attention to the processes producing resemblance between groups is necessary for the proper interpretation of group-selection events.

The degree of altruism that evolves in a population depends on the balance of opposing forces at the group and individual levels. Because W & S focus on kin groups only as *vehicles* of selection, however, they give an incomplete account of why kin groups are more favorable for the evolution of altruism than groups of unrelated individuals. The evolutionary response to any form of selection depends both on the strength of the applied selection pressure and on the degree of resemblance between units of selection in different generations. Figure 3 in the target article shows that the variance in altruist frequency among groups is greater for groups composed of siblings (kin groups) than for groups formed from unrelated individuals (random groups). As a result, the variance in group fitness is greater among kin groups than among random groups, but this is not sufficient to guarantee conditions more favorable to the evolution of altruism in kin groups than in random groups. To see why, consider an example of individual selection.

Imagine two populations of plants in which individual fitness is positively correlated with height, tall plants being more likely to survive than small plants. Suppose, however, that all individual differences in height are environmentally induced, and that the variance in height increases as the density of neighbors increases. Population A is relatively sparse, so the variance in plant height is relatively small. Population B is dense, so the variance in plant height is relatively great. Clearly, greater variation in height in population B implies stronger selection on height in population B than in population A. Do we therefore expect a greater response to selection in population B than in population A? Obviously not, because in neither population is there any relationship between the height of a parent plant and the height of its progeny. For a process of natural selection we require not only differences among individuals that are causally related to survival and reproduction, but also differences that can be transmitted from parents to progeny.

If adaptation at the group level requires a process of natural selection operating at that level (cf. sect. 1.2; Williams 1993), then groups must do more than serve as vehicles of selection. Just as a process of natural selection at the individual level requires that individual differences be heritable, so the characteristics of groups that cause them to differ in fitness must be heritable at the group level if a process of natural selection is to occur at the group level. Only if the groups in which progeny find themselves resemble those in which their parents found themselves can there be an evolutionary response to the selection imposed at the group level. In short, for a process of natural selection to occur at the group level we require that the group be both a *vehicle* of selection and a *replicator*. And for a characteristic to count as a group-level adaptation we require that it have arisen through a process of natural selection in which groups acted both as vehicles and as replicators.

Kin groups differ from random groups in one way that W & S did not notice. They are replicators. The progeny produced by individuals developing in kin groups with a high frequency of altruists will also tend to find themselves in groups with a high frequency of altruists, and those produced by individuals developing in kin groups with a low frequency of altruists will tend to find themselves in groups with a low frequency of altruists, but there will be no relationship between the frequency of altruism in parental and offspring groups when those groups are formed at random. Parental kin groups resemble offspring kin groups because of the predictable relationship between a parent's own

genotype, the type of group into which it was born, and the genotype of its offspring, from which its offspring's kin group is formed. There is no such relationship between parental and offspring groups when they are formed by a random draw. In short, there is heritable variation *at the group level* for fitness among kin groups, but not among random groups (assuming they are broken apart and reformed every generation).¹ Thus, altruism that evolves through kin selection is a group-level adaptation. Altruism that evolves in a population with randomly structured groups is not, even if those groups serve as vehicles of selection.² Kin group organization is one way, among many, by which heritable between-group differences may arise.

Wilson & Sober argue persuasively that the small social groups characteristic of human populations for much of our evolutionary history may have served as vehicles for group selection. As a result, it is certainly worth considering whether some characteristics of human behavior that are difficult to understand on an individualistic basis are better interpreted as group-level adaptations. In doing so, however, we must be careful to check not only that groups could have served as an appropriate vehicle for such selection, but that they had the means to replicate themselves.

NOTES

1. There is some heritability of between-group differences with randomly structured groups, but it is much smaller than the heritability of between-group differences with kin groups. If groups with a high frequency of altruists are more productive, on average, than groups with a low frequency of altruists, their progeny will be found in groups with a broader range of altruist frequencies. If the overall frequency of altruism changes between generations, the progeny distribution of individuals from altruistic groups will be more truncated than that from nonaltruistic groups. This leads to a weak association between the frequency of altruism in parental and offspring groups. In short, there will always be some degree of heritability for traits at the group level if those traits are heritable at the individual level. The important question, therefore, is whether the magnitude of that heritability is so small as to prevent a meaningful evolutionary response to selection at the group level.

2. Strictly speaking, there will be some component of group-level adaptation to altruism that evolves with random groups. Adaptation at the group level is likely to have played a minor role in the evolution of altruism under these conditions, however, because the heritability of between-group differences is so small.

Taking vehicles seriously

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Periodic reconceptualizing areas of science to introduce greater coherence is as necessary as it is difficult. Wilson & Sober (W & S) propose to restructure our understanding of selection processes centering on the concept of vehicles, not replicators, and they supply a means by which one can decide which levels of organization are functioning as vehicles at any one time. Although I find myself in basic agreement with W & S's position, I think that one aspect of their exposition is extremely misleading. They write as if they accept Dawkins's (1976) distinction between replicators and vehicles, when actually they transform it significantly.

According to Dawkins, replicators pass on their structure through successive replications. Obviously, Dawkins developed his notion of a replicator with genes in mind, but I disagree with W & S when they say that "all genes are replicators by definition." Dawkins's definition certainly lends itself to genes, but nothing in it requires that genes and only genes fulfill his requirements. Dawkins does go on to argue that genes are the only replicators, but he has to append these arguments to his definition.

In the beginning, according to Dawkins, the original replica-

tors might have been naked genes, but eventually genes constructed vehicles of various sorts to aid them in their task of replicating themselves. For Dawkins, the connotations of the term "vehicle" are appropriate. He sees all-powerful replicators riding around in the vehicles that they construct and direct, discarding them for new survival machines when the occasion demands. Dawkins is certainly a gene *replicationist*, but he is also a gene *selectionist* only if he thinks that replication is not just necessary but also sufficient for selection. In his later publications, Dawkins (1982a; 1982b) makes it clear that he does not. Vehicles also play an important role in selection. They form a hierarchy of increasingly inclusive vehicles. As everyone now seems to agree, the levels-of-selection controversy does not concern replicators but vehicles, or what I have termed "interactors" (Brandon & Burian 1984; Dawkins 1982a; 1982b; Eldredge & Grene 1992; Hull 1980; Lloyd 1988; Williams 1985).

W & S treat Dawkins's "vehicle" and my "interactor" as synonymous, but as Dawkins and I have defined these terms, they are not. As Dawkins sees it, the primary relation between replicators and vehicles is developmental. Replicators produce vehicles of increasing inclusiveness. The replicator-vehicle distinction mirrors the genotype-phenotype distinction. As a result, replicators cannot themselves function as vehicles: replicators both produce and control vehicles but cannot themselves be vehicles. Genes cannot ride around in themselves, nor are they lumbering robots. Thus, if "vehicle," as W & S use the term, allows genes to be vehicles and Dawkins's usage does not, W & S must have transformed the meaning of this term in ways that remain only implicit in their exposition.

Although I cannot deny that the gene-organism relation also influenced how I originally conceived of the replicator-interactor relation (Hull 1988b, p. 256–57), from the first I defined "interactor" in terms of the role that interactors play in selection, not development. As I defined this term, an interactor is an "entity that interacts as a cohesive whole with its environment in such a way that this interaction *causes* replication to be differential" (Hull 1988a, p. 134; see also Hull 1980, p. 318 and 1988c, p. 408). Thus, no entity is in-and-of-itself an interactor. An entity *functions* as an interactor depending on the role it plays in a particular selection process. An interactor must *cause* replication to be differential, but the causal mechanisms involved can vary. According to my definition, genes themselves can function as interactors. They can interact with their biochemical and cellular environments in such a way that they themselves are replicated differentially. Although Dawkins (1982b, p. 46) now doubts that the effects of genes need to be bundled together in discrete vehicles, he still conceives of vehicles as "units of phenotypic power of replicators" (Dawkins 1982b, p. 51). Dawkins is willing to talk loosely about phenotypic traits being "for" something (e.g., bird wings for flying), but not DNA. DNA codes for phenotypic traits, but DNA itself is not "for" anything. Even in Dawkins's extended usage, genes cannot function as vehicles.

According to W & S, the "essence of the vehicle concept is *shared fate*." The method that W & S use to decide the level at which interaction is taking place has much in common with the "additivity" method first suggested by Wimsatt (1980; 1981) and later developed extensively by Lloyd (1988). I wish that W & S had gone on at greater length about any similarities and differences that their method has in contrast to that of Wimsatt and Lloyd.

In sum, Dawkin's terminology lends itself to the claim that genes are the units of selection. W & S counter that vehicles are the units of selection. According to the terminology I prefer, *there are no units of selection* because selection is composed of two subprocesses – replication and interaction. Selection results from the interplay of these two subprocesses. Genes are certainly the primary (possibly sole) units of replication, whereas interaction can occur at a variety of levels from genes and cells through organisms to colonies, demes, and possibly

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 out-group 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. Altruism₁ 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. Altruism₂ 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 altruism₂ necessary for survival. Given the very low population density of archaic humans it is unlikely that there would have been much opportunity for altruism₁, and although it is possible to envisage scenarios where altruism₁ 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 altruism₁ 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 altruism₁, such as Christianity, had an impact 2,000 years ago because they promoted altruism₁ when this was not an accepted philosophy (Ling 1968). It is of course possible that altruism₁ is the consequence of generalization of altruism₂ (loved ones and strangers share human features), or it may be that the philosophical principles of altruism₁ have developed independently of evolution. Nevertheless, although the parliament of a religious order that requires altruism₁ 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 altruism₁ had a positive influence on group survival. By contrast, the trait of altruism₂ can be explained in terms of group selection because it would have supported archaic hunter-gatherer survival. Altruism₂ 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 altruism₁, 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 altruism₂. Wealth-owning, farming communities would have favored traits of competitiveness toward strangers but would not have selected against altruism₂. Altruism₁ certainly exists, as examples cited by W & S show, but it is not easy to see how altruism₁ 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 Smith'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-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-

trol of resources: one of the virtues of W & S's approach is that fitness differences need not be concentrated at one level of the biological hierarchy.

1. Dimensions of group evolutionary strategies. This theoretical indeterminism is also critical in conceptualizing human group evolutionary strategies. Human group evolutionary strategies, such as those of the Hutterites discussed by W & S, are "social organizations that we build for ourselves," what I term "experiments in living" (MacDonald, 1994) in which general purpose cognitive mechanisms may be used in an attempt to achieve evolutionary goals (MacDonald 1991). There are no theoretical limits on how such strategies may be constructed, although, as W & S suggest, there are theoretical reasons to suppose that some types of strategies are likely to fail. In the following I will discuss several independent dimensions of group strategies and illustrate them with reference to the Hutterites, as discussed by W & S (sect. 3, para. 3), the Spartans (MacDonald 1988a; pp. 301–4), and the Jews (MacDonald 1994).

1.1. A dimension ranging from complete genetic closure in which the group is closed to penetration from other individuals or groups at one extreme, to complete genetic openness (panmixia) at the other. The Hutterites originated as a group of genetically unrelated families; the Jews and the Spartans developed as groups with ethnic/national strategies in which there were cultural barriers against genetic penetration from surrounding peoples. Population genetic data indicate that Jews have remained genetically distinct from the groups they have lived among for centuries. In addition, Jewish populations from widely separated areas have significantly more genetic commonality than is the case between Jews and the gentile populations they have lived among for centuries.

1.2. A dimension ranging from high levels of within-group altruism and submergence of individual interest to group interests at one extreme, to complete within-group selfishness at the other. The Hutterites, Spartans, and Jews all range toward the altruistic end of this dimension. Jewish economic activities have often been characterized by a high degree of nepotism and within-group charity. Group interests were of primary importance rather than the interests of individual Jews, as indicated, for example, by laws preventing competition between Jews doing business with gentiles.

1.3. A dimension ranging from high between-group resource and reproductive competition at one extreme, to very little between-group resource and reproductive competition at the other. Group-level adaptation sets the stage for between-group resource and reproductive competition. Nevertheless, by continuing to use outmoded technologies, it is possible that groups such as the Amish dampen intergroup competition. Resource competition between Jews and gentiles has often been intense and has resulted in group differences in reproductive success. Resource competition has occurred in a wide range of activities, including artisan guilds, money lending, trading, manufacturing, education, the professions, and influence on the government.

1.4. A dimension ranging from high levels of ecological specialization at one extreme to ecological generalization at the other extreme. Whereas the Hutterites appear to specialize in agricultural production and the Spartans specialized exclusively in military activities, Judaism has been characterized by eugenic practices resulting in cultural and natural selection for intelligence and high investment patterns of child-rearing.

2. Proximal mechanisms facilitating group strategies. W & S argue that social identity research (e.g., Hogg & Abrams 1987) suggests that there are evolved psychological mechanisms that predispose individuals to join or form groups, which result in group-level adaptive processes. It is noteworthy that social identity processes are exacerbated by real conflicts of interest (see also Sherif 1966; Triandis 1990, p. 96), data highly compatible with the hypothesis that social identity processes are facultative in the sense used by evolutionists. This facultative response to external threat has often been manipulated by Jewish authorities attempting to inculcate a stronger sense of group identifica-

tion among Jews by exaggerating the threat of anti-Semitism (Hartung 1992; MacDonald 1994; Wooscher 1986). Strategizing groups are thus able to manipulate social environments in ways that trigger evolved psychological mechanisms related to group functioning. On the other hand, there are several important historical examples where increased levels of resource competition between Jews and gentiles have triggered reactive processes among gentiles, resulting in gentiles developing highly cohesive anti-Semitic group strategies in opposition to Judaism – what I term "reactive racism" (MacDonald 1995).

Social identity processes appear to be a pan-human universal, but there are important individual differences in the tendency to form cohesive groups (see Triandis 1990, 1991 for reviews). Collectivist cultures (and Triandis 1990, p. 57) explicitly includes Judaism in this category) place a high emphasis on the goals and needs of the group rather than on individual rights and interests. Socialization in collectivist cultures stresses group harmony, conformity, obedient submission to hierarchical authority, and honoring parents and elders. As in the case of social identity processes, there is evidence that collectivist tendencies become more pronounced during periods of group conflict (Triandis 1990, p. 96).

Beyond shared fate: Group-selected mechanisms for cooperation and competition in fuzzy, fluid vehicles

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Abstract: This commentary makes two points about group selection. First, selection can certainly act on vehicles of various kinds, but applying this idea to human groups is tricky, because a human group is such a fluid, fuzzy sort of vehicle. Nevertheless, even without shared fate, human groups can use "resource levellers" and "resource lotteries" to foster cooperation. Second, vehicles can exploit internal competition as well as internal cooperation to promote their efficient survival and reproduction, so adaptations for meritocratic sexual competition within human groups, as well as adaptations for egalitarian cooperation, may have been favored by group selection.

1. Resource levellers and resource lotteries as group-selected mechanisms for human cooperation. Classic examples of evolutionary vehicles, such as multicellular bodies and multi-insect colonies, share several features: (1) high genetic relatedness among constituent individuals; (2) a physically integrated vehicle structure (a body or hive) that imposes a shared fate on the constituent individuals; and (3) an obligate division of labor between germ-line individuals (e.g., sperm and egg cells or hive queens) and somatic individuals (e.g., somatic cells or sterile workers). Human tribal groups make unusual vehicles because they lack these three features: human group selection differs from kin selection by definition because of the low genetic relatedness of individuals in the group; humans probably did not construct group vehicles (e.g., village stockades) until recently, and no human group, not even the Hutterites, has a happy, consensual division of labor between a reproductive caste and a sterile caste. Rather, human tribal groups have genetic, social, cultural, linguistic, and spatial boundaries that are fuzzy and fluid. Theories of human group selection must therefore explain how selection can favor cooperation in fuzzy, fluid, facultative vehicles that do not have a genetic identity, a vehicle phenotype, or a separate germ-line. In groups composed of individuals who can survive, reproduce, and migrate separately, shared fate can erode and selfishness can win out.

Shared fate really means shared fitness: the vehicle's structure in relation to its environment ensures that fitness is highly correlated across individuals within the vehicle. Sometimes,

pack-hunting predators or genocidal group warfare may have imposed true shared fate on ancestral human groups. Most shared fate in modern human groups, however, depends on fairly recent technology, such as ropes to tie mountain-climbers together, or real "vehicles" to navigate land, air, and water (such that "we're all in the same boat"). The fluidity of tribal groups and the autonomy of individuals suggest that human groups created moderately correlated fitnesses among their members, rather than truly shared fate.

Without obligate shared fate, there seem to be two main ways to promote cooperation in human groups: (1) "resource levellers" that distribute resources obtained by group cooperation fairly equally across individuals, and (2) "resource lotteries" that make the distribution of fitness benefits resulting from group cooperation unpredictable at the moment that individuals commit to cooperate. Resource levellers probably work best for cooperative tasks that impose low risks and low costs on individuals, whereas resource lotteries work best for those that impose high risks and high costs. Because Wilson & Sober (W & S) discuss resource levellers such as egalitarian ideology and food sharing at some length, I will focus on resource lotteries, as introduced and analyzed by Tooby and Cosmides (1988; 1993).

Resource lotteries work best when cooperation produces individual payoffs with a positive mean value and a high variance, with positive and negative outcomes that are fast, final, unpredictable, and unshareable (such as successful fertilization or death). These conditions make it foolish to defect before the lottery and impossible to defect afterward. The main resource lotteries in human evolution were probably cooperative hunting, cooperative warfare, and cooperative sexual coercion. For example, Tooby and Cosmides (1993) suggested that the development of projectile weapons may have facilitated the evolution of human cooperative warfare, by making the outcome of warfare more unpredictable to the individual but more beneficial to the winning group. A fast hail of projectiles imposes a less predictable survival lottery than an afternoon of hand-to-hand combat, so individual defection is less likely. Likewise, prey animals that have evolved "protean" abilities to flee and counter-attack unpredictably (Driver & Humphries 1988; Miller & Freyd 1993) impose a survival lottery on cooperative hunters. Moreover, warriors or hunters may draw lots at random to decide who will lead a dangerous raid. Cooperative sexual coercion by males can also function as a reproductive lottery, because the outcome of sperm competition among multiple males is not predictable (see Bellis & Baker 1990).

W & S do recognize the analogy between meiosis at the genetic level and randomization mechanisms for ensuring cooperation at the group level, and mention the Hutterite lottery method for assigning the original home site to one of two groups after splitting. Even John Rawls (1971) used a resource lottery argument to support his resource-levelling theory of political justice, when he asked how one would want society to be structured if one's birth position (family, sex, class, and race) were to be determined at random. Because the importance of adaptive unpredictability in biology and psychology has been long overlooked (Driver & Humphries 1988), the study of unpredictable resource lotteries to promote group cooperation may be a fruitful area for further research. Rapoport and Budescu (1992) have already demonstrated that individual humans are rather good randomizers under ecologically valid conditions; perhaps human groups are too.

2. Cultural courtship systems as group-selected mechanisms for efficient sexual selection. My second main point is that efficient vehicles use internal competition as well as internal cooperation to organize and maintain functional adaptations. Multicellular bodies exploit competition in many ways: brain development depends on competition between neurons for neurotrophic signals, learning depends on competition between synapses for reinforcement, and immune system functioning depends on differential reproduction between antibodies in favor of superior antigen-matches (see Gazzaniga 1993). At the

level of human groups, then, group selection itself may favor a subtle balance between egalitarian collectivism and eugenic meritocracy. Some apparently selfish behaviors such as role differentiation, status seeking, and sexual competition may have been favored by group selection, just as certain modes of competition between neurons and between anti-bodies were favored by individual selection.

In particular, group selection between human tribes may have favored ritualized modes of sexual competition and courtship that promote efficient mate choice, thus amplifying differences in reproductive success and maintaining the tribe's gene-pool quality across generations. Whereas resource levelling and resource lotteries promote group cooperation within a generation, amplifying reproductive differences through meritocratic sexual competition promotes group eugenics across generations. Consider two hypothetical tribes of equal size, cooperativeness, and technology: the Random Maters enforce random mating and equal numbers of offspring among all its surviving men and women, whereas the Selective Breeders encourage selective and assortative mating, meritocratic polygamy, and higher numbers of offspring for higher-viability men and women. Across generations, we would expect group selection itself to favor the Selective Breeders, who coevolve against pathogens, propagate heritable innovations, and guard against recurrent deleterious mutations much more efficiently than the Random Maters do. The idea that group selection can favor group-level eugenics has bad historical connotations, but eugenics is what selective mate choice is all about, and any group mechanisms that promote efficient mate choice, such as parties, feasts, dances, sporting contests, religious rituals, political rallies, and scientific conferences, may serve a eugenic function for the group. Individual selection and group selection can sometimes reinforce one another, creating powerful evolutionary pressures on organisms (and difficult methodological problems for biologists.)

Of course, the Random Maters might gain an advantage if egalitarian mating fostered better group cooperation and if technological and economic innovations made this short-term cooperation much more important than long-term sexual-selective efficiency. This may help to explain the otherwise mysterious historical shift from polygynous, hierarchical medieval cultures to more monogamous, egalitarian capitalist cultures in Europe (Betzig 1986). More often, though, we might expect group selection to push toward egalitarian collectivism in survival domains but eugenic meritocracy in reproductive domains. Indeed, many human groups have developed cultural distinctions between collective rituals to promote group cooperation in survival domains and ritualized courtship competitions to promote meritocratic selective mating in reproductive domains. The classical liberal principle of "equality of opportunity, inequality of outcome" also strikes a balance between cooperation-promoting egalitarianism and competition-promoting meritocracy. This balance may have been favored by group selection: whereas economic individualists probably starved to death, reproductive communists were probably mutated into collective oblivion. Our ancestors may have prospered, as individuals and groups, by combining tender economic socialism with tough reproductive libertarianism. This hybrid system may reflect a conflict between different group-selection pressures over different time scales, not just a conflict between levels of selection. If so, group selection may have favored group cooperation that buffered individuals from natural selection by the external environment, but it may have increased the intensity of sexual selection through mate choice, thereby setting the stage for runaway sexual selection in human mental evolution (see Miller 1993; Ridley 1993).

Hominids, coalitions, and weapons: Not vehicles

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Abstract: Pace Wilson & Sober, group selection has not won over biology. However, the combination of fission/fusion organization (favoring coalition formation and relatively complex tactical behavior) with weapons (which in conjunction with group or ambush attacks greatly reduce the costs to actors of lethal inter- and intragroup aggression) create circumstances that may well have favored group selection in hominid evolution.

Wilson & Sober's (W & S's) target article is based on two fundamentally flawed premises:

First, that group selection has been widely accepted in biology and that the social sciences are in need of the good news. This is belied both by their list of prominent "holdouts," and by their own pleas with "gene-centered theorists" to offer recognition: "All of the major developments . . . are over ten years old and it is time for them to be acknowledged generally" (sect. 1.6, last para.). Regardless of the merits of their hypothesis, or the injustice of dismissal by silence they may be suffering, their stated purpose is [self?]deceptive.

Second, that the question "at the heart of the group selection controversy [is] can groups be like individuals in . . . harmony and coordination?" . . . (sect. 1.3, last para.). Even G. C. Williams agrees that group selection *can* work (see Note 4, and compare with sect. 1.4.2, para. 3); this is not controversial. Debate centers on which groups, how often, and why. I do not accept the idea that W & S's perceived conflict between group and individual perspectives in this debate is necessarily substantive simply because "it refuses to go away"; so does nature/nurture.

As a result, W & S's paper fails in its attempt to establish sophisticated group selection as an important part of the reigning biological paradigm. Happily, however, it does "reintroduce group selection to the human behavioral sciences," and this at least is worth serious consideration. Humans display many behaviors that appear difficult to explain in individual selection terms. Might group selection have been important in *human* evolution, if not in evolution in general?

It is important to emphasize that individual selfishness is capable of producing cooperation and apparent "altruism." Among adult mammals at least, mutualistic game-theoretical explanations for cooperation have generally proven superior to those based on reciprocity or nepotism (e.g., Bercovitch 1988; de Waal 1982; Moore 1984; Packer & Pusey 1982), though lack of genetic data often makes discrimination among explanations difficult (e.g., Connor et al. 1992; see Moore 1992). However, a variety of human traits are difficult to explain via individual selection (e.g., "indoctrinability" or "religiosity"; note that I say difficult, not impossible).

The leading scenario for the evolution of such traits was set out by Darwin (1871) and significantly elaborated by Alexander (1985; 1989). According to them, violent intergroup conflict provided the selection pressure that ultimately resulted in group-directed altruism; as Darwin put it,

A tribe including many members who, from possessing in a high degree the spirit of patriotism, fidelity, obedience, courage, and sympathy, were always ready to aid one another, and to sacrifice themselves for the common good, would be victorious over most other tribes; and this would be natural selection.

Although both authors favor individual-level explanations for the evolution of these "traits" (*sensu lato*), it is not hard to see how W & S's group-selection ideas might apply. (Note that the one example of possibly group-selected cooperation offered by

Mesterton-Gibbons & Dugatkin (1992, p. 274) is of ants in which "[i]ntracolony cooperation . . . appears to be the result of inter-colony aggression.")

The Hutterite example given is particularly instructive, as they are cognitively manipulating migration rates by identifying and expelling noncooperators. If rook flocks were closed and individuals collectively attacked pairs laying large clutches, Wynne-Edwards would have carried the day. Manipulation combined with explicit indoctrination results (indirectly) in high reproductive success for all members, relative to non-Hutterites, apparently *limited only by intergroup competition* ("persecution and legal restrictions"). An interesting thought experiment: remove all non-Hutterites from Canada, seal the borders, and wait until the habitat is saturated.

Because many animals live in groups and could in principle evolve the required mental attributes, why have humans gone so far down the potentially group-selected path? What is different about us?

Manson and Wrangham (1991) argue that the potential for lethal intergroup violence is great in chimpanzees and humans because subgrouping creates the potential for imbalances of power: a party from one community can attack an individual of another at relatively low cost to themselves. For chimpanzees, they further argue that the ability of a party to physically immobilize a lone opponent lowers the cost of aggression still more.

For chimpanzees, such attacks are protracted and the victims often survive (Manson & Wrangham 1991). Now imagine such an attack by a group of hominids carrying stone weapons. The impact, as it were, of such tools cannot be overemphasized. Here is what is different about us (as with other traits, a difference in degree, not kind): the combination of coalitions plus weapons vastly increases the potential for lethal aggression, and to the degree that fission/fusion processes have characterized hominids, this potential is increased even more.

The introduction of weapons makes us different in another way. Although the basic parameters leading to the evolution of "egalitarian" societies are general (Vehrenkamp 1983), coalitions and weapons greatly increase the difficulty of achieving despotic power in nonstate society. Cooperatively enforced sanctions (including assassination) against those who attempt to manipulate power or resources for personal benefit are widespread in small-scale "egalitarian" human societies; they may explain the existence of such societies, and are fully interpretable in individual selection terms (Boehm 1993). Hutterite exclusion of noncooperators is an example of such status levelling in human groups.

The potential importance of the relations among fission/fusion organization, coalitions, and social complexity in the evolution of cognitive complexity is widely recognized (e.g., Alexander 1989). A strong case can be made as well that hominids have taken this path further than chimpanzees or bottlenose dolphins because of the discovery of weapons, which (in combination with the foregoing) drastically change the costs of aggression and so the complexity of intra- and intergroup relationships. I note, speculatively, that (1) the first stone tools, (2) a major increase in encephalization, and (3) a so-far unexplained thickening in the cranial vault bones all coincide with the origin of *Homo*, and that *H. erectus* soon followed, characterized by a further thickening of the cranial vault and an apparently abrupt increase in stature (see Klein 1989; Wood 1992). Space precludes elaborating on the obvious. [See also Falk: "Brain Evolution in *Homo*" BBS 13(2) 1990; Dunbar: "Coevolution of Neocortical Size, Group Size and Language in Humans" BBS 16(4) 1993.]

In conclusion, human behavioral biologists *will* profit from considering Wilson & Sober's ideas, but only after reading Alexander (1989) and others and thinking about why humans are (quantitatively) different from other organisms in game-theoretically relevant ways.

Why is group selection such a problem?

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Abstract: The controversy over group selection persists not, as Wilson & Sober argue, because biologists do not understand the hierarchy of vehicles of selection, but because we lack criteria to determine whether or not a trait arises from group selection, and have a deep wish to find a biological basis for our human moral feelings.

Group selection? Still? More? Again? Despite dozens of articles and books on the topic, fundamental disagreements persist. Such intractability usually arises from failure to conceptualize a problem clearly, lack of data, or the influence of political or emotional factors. In the curious case of group selection, all three factors conspire to maintain confusion.

Wilson & Sober (W & S) claim that "overextended definitions of individual and gene selection have misled a generation of biologists into thinking that natural selection almost never occurs at the level of groups" (sect. 1.6) and they set out to "rebuild inclusive fitness theory on the foundation of vehicles" (sect. 1.5). They go to great lengths to show that groups, like individuals, can be vehicles for natural selection. But this is not at issue, is it? Wilson and others have described models in which genes that benefit a group can be selected for even though they decrease an individual's inclusive fitness. These models work, albeit under very restricted conditions. The question is not whether traits that benefit the group at the expense of the individual are possible; the question is whether they are important, and especially whether they can account for human altruism.

This brings us to the paucity of data. The authors use starving rabbits on tiny islands to illustrate the principle, but the lack of evidence for such population limitation is the very spark that kindled the demise of naive group selection. The aberrations from equal sex ratios are intriguing, but no mention is made of alternative explanations for these findings. The Hutterite example, although atypical for the species, proves that humans can be extraordinarily altruistic, but it says nothing about the mechanisms that make this possible, and nothing about the selection processes that shape these mechanisms.

W & S address the core question of whether organisms (especially humans) have traits (especially altruism) that were shaped by the force of selection acting at the group level despite selection against these traits at the individual level. The conceptual problem here seems to me to have little to do with vehicles and everything to do with standards of evidence. How can we tell if a trait arose by this process or some other one? We can not. There is no phylogeny to trace, no comparative information to guide us. If someone could demonstrate a trait that decreased inclusive fitness and increased group fitness, we would have a good start, but I know of no such trait.

As for George Williams, he may have led us out of the wilderness of naive group selectionism, but I doubt that he would endorse the Commandment offered in his name: "Thou shalt not apply the adaptationist program above the level of the individual." Instead, he simply applies Ockham's razor and insists that we explain phenomena at the simplest possible level. He also insists that we carefully distinguish the information (the codex) that is changed by natural selection from the material domains in which that information resides. He notes that, "a gene is not a DNA molecule; it is the transcribable information coded by the molecule . . . a whole addictive organism . . . is not really an object, it is a region in which certain processes take place" (Williams 1992, p. 11). He is well aware that selection can take place at levels other than the genes and the individual. His 1992 book contains some fine examples of clade selection, for example, Van Valen's evidence that individual mammals are selected for larger body size, but clades of mammals with large

bodies are constantly being supplanted by those with smaller bodies.

What about vehicles of selection? The strategy of moving up the hierarchy until one finds fitness differences between vehicles is helpful, but, as the authors say, "fitness differences are not always concentrated at one level of the biological hierarchy. . . . In these cases, we cannot assign the status of organ, organism, or population and must settle for some hybrid designation" (sect. 1.4). Exactly. Except in boring cases, the analogy fails. Viewing selection from the gene's perspective is a great advance precisely because it highlights and explains the complexities that arise when one force of selection favors a gene and another opposes it. Some, but not all, of the best examples arise from conflict between levels of the hierarchy. "Outlaw genes" foster their own success at the expense of the individual. The disadvantage they pose to the individual selects for opposing "police genes," like those that mediate crossing over to separate outlaw genes from their conspirators. The interesting question at the heart of W & S's target article is whether the power of group selection is sufficient to select for genes that cause any appreciable harm to individual inclusive fitness. The consensus has been "probably only rarely." One reason, surprisingly not addressed by the authors, is the fundamental difference between an individual organism and all higher levels of organization. All the cells in the individual share the same genetic information, and thus have their interests in common. Higher-level vehicles have genetic differences, so, in all but the most special circumstances, genes that favor the interests of the group over the individual will be replaced by genes that favor the interests of the individual and its genes.

Conflicts within the level of the individual are equally important because they go further toward replacing the notion of an organism as a perfect creation with a more realistic picture of an organism as a bundle of compromises, and because such conflicts often give rise to disease. In heterozygote advantage, a gene gives enough of an advantage to some individuals to outweigh the disadvantages of disease that arise in other individuals who have two copies of the gene. In antagonistic pleiotropy, a gene offers a benefit and a cost to the same individual. Some, like DR3, increase the likelihood of uterine implantation and retention, but later cause disease, in this case, diabetes. Other genes give a selective advantage in youth that outweighs their later contributions to senescence. Then, of course, there are kin-selected genes that code for behavioral tendencies to assist relatives who share genes identical by descent, thus decreasing the individual's fitness, but increasing inclusive fitness. Although groups in which kin altruism exists may have an advantage over other groups, the fitness differences that select for kin altruism are between individuals, not groups. By contrast, genes that foster reciprocity exchanges impose a cost on an individual in the short run, but give an advantage in the long run (depending on the strategies used by other players and the ability to detect and remember behaviors by others). In all these examples, the conflict is between two effects of the gene in the same individual, or between the effects in two different individuals, not between different levels of the hierarchy.

Enough of conceptual and data problems; what are we to make of the fervor of the quest to demonstrate group selection? W & S seem determined to demonstrate that human altruism arises from group selection. I sympathize with their wish. The discovery that tendencies to altruism are shaped by benefits to genes is one of the most disturbing in the history of science. When I first grasped it, I slept badly for many nights, trying to find some alternative that did not so roughly challenge my sense of good and evil. Understanding this discovery can undermine commitment to morality – it seems silly to restrain oneself if moral behavior is just another strategy for advancing the interests of one's genes. Some students, I am embarrassed to say, have left my courses with a naive notion of the selfish gene theory that seemed to them to justify selfish behavior, despite

my best efforts to explain the naturalistic fallacy. Is selfish-gene theory a meme that is toxic to social structures that depend on commitment to abstract moral principles? I worry a lot about this possibility and thus sympathize with those who want to show that human altruism was shaped by group selection. If this were true, it would help, psychologically at least, to reconcile our moral feelings with our biological natures. Unfortunately, it seems to be false.

Nongenetic and non-Darwinian evolution

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The hierarchy of vehicles underlying the main thesis of Wilson & Sober's (W & S's) target article corresponds to the hierarchy underlying so-called organismic system theory, which explores analogical features of structure, function, and evolution of an organism's subsystems (e.g., the cells, tissues, or organs of an individual) and its supersystems (populations, species, ecosystems, groups, societies, nations, etc.).

In the context of human evolution, this exploration is especially relevant to the issues discussed by W & S, because it reveals how our species is unique in a very special sense, namely, we produce and are subjected to an evolutionary process, which is independent of natural selection acting on genes or on vehicles generated by their action.

Consider the taxonomic tree of languages, a direct analogue of the corresponding tree of biological taxa. Both trees portray an evolutionary process. A compelling reason for assuming independence of language evolution from biological determinants is the salience of mechanisms of reproduction and selection apparently unrelated to adaptation in the sense of enhancing the reproduction of genes.

To fix ideas, consider a possible mechanism of the phonetic evolution of a language. Let the phone be the "replicator." Let imitation of the produced phone by other speakers represent reproduction. Let slight changes in the phone play the part of mutations. If the changed phone is easier to pronounce and entails no significant loss of information content, it will be imitated by more speakers and will eventually replace the original one (analogues of differential reproduction rates produced by natural selection). If we suppose that written language is "more conservative" than speech, we can assume that our model is corroborated by the abundance of "silent letters" in English orthography, vestigial parts that have remained functional in German, for example (cf. Knecht - knight; Tochter - daughter, etc.).

As another example, consider the evolution of artifacts. The "fossil histories" of implements, weapons, articles of clothing, vehicles, and so on can be seen in any museum, revealing striking analogies to the evolution of animals even to vestigial parts. The "horseless carriage" still had a stand for a whip. The automobile "reproduces itself" quite literally on the assembly line. Models that sell well enjoy a reproductive advantage and eventually replace those that do not. Witness the extinct specimens.

Our examples can be regarded as generalizations of Darwinian evolution in the sense that the processes are driven by a kind of reproduction and a kind of selection. They can be called quasi-Darwinian. Evolutionary processes independent of selection based on differential reproduction rates can be called non-Darwinian.

Evolution of systems exemplifies such processes. A system can be defined as a portion of the world that, in spite of far-reaching internal changes, remains "itself." Surely living individuals are examples. Their material constituents are continu-

ally replaced, yet their identities are unmistakable. We humans have direct evidence of our own identity – our memories. There is no difficulty in assuming continued identity of larger organisms, species, groups, organizations, states, even conceptual systems like languages, religions, or scientific theories.

Can one ascribe "adaptation" to such systems, on which their continued existence (preservation of identity) depends? I think we can if we separate adaptation from competition (i.e., differential reproduction rate), the most fundamental concept of Darwinian evolution. This separation justifies calling some evolutionary processes "non-Darwinian" with reference to the level on which differential reproduction rates do not occur. Thus, languages can hardly be said to engage in a survival of the fittest reflected in differential reproduction rates. However, the evolution of a language can be said to be driven by an *internal* quasi-Darwinian process, for example, differential reproduction rates (imitation frequencies) of phones, perhaps also of syntactic and semantic features.

Adaptation of a system to its environment need not be manifested in a superior reproduction rate. It can be evidenced simply by longevity. Successfully adapting systems are still around; those that did not adapt are no longer with us. Consider a firm, an institution, or a religion, that has preserved its identity (is recognized as "itself") for a long time. To say that it has been adapting to its environment is almost a tautology. The interesting question is how. The viability of such a system depends on the support it gets from its environment. A store needs customers, a political party voters, a religion adherents. Support is mobilized by policies, and these are designed and carried out by personnel. Consequently, "adaptation" consists of selecting the personnel recruited into the system. This is the internal analogue of a "Darwinian" process that enhances the survivability of the system by guiding its evolution, which on the higher level appears to be non-Darwinian.

I believe the question of group selection should be defined with reference to the level of analysis. If selection is defined in the strict Darwinian sense, then a case against group selection can be made if the evolutionary success of a group cannot be shown to be a consequence of differential reproduction rates of groups. Survivability of groups (at least human groups) need not depend on reproduction. It does depend on adaptability to environment, however, and this is where the uniquely human repertoire of adaptability methods introduces an entirely new dimension into evolutionary theory.

In directing attention to the vehicle of selection (rather than fixating on the gene as the fundamental replicator), Wilson & Sober open the way to a multilevel theory of selection, thereby providing a theoretical underpinning to group selection. In the context of the evolution of human social behavior and organization, the generalization could go a step further. We can recognize and examine processes that are quasi-Darwinian but not genetic in the sense of being driven by differential reproduction of replicators that are not genes. (Learning may be a further example if we suppose that it is based on differential reinforcement and inhibition of neural circuits.) And we can examine non-Darwinian evolutionary processes – those driven by adaptation to an evolving environment but not by differential reproduction rates.

Adaptation and natural selection: A new look at some old ideas

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Abstract: The debate between individual- and group-selection perspectives centers on the *probability* that group selection played a major role

in evolution, which may depend on the species being studied. To explore the viability of group selection for altruism, I present fitness indexes for altruists, nonaltruists, and groups when the parameters of costs, benefits, and proportion of altruists in a group are varied.

Wilson & Sober (W & S) present a case for "reopening" the debate about whether group selection played a pivotal role in evolution. The crux of this debate centers on Williams's (1966) three major arguments against the viability of group selection: (1) higher-level adaptations necessitate higher levels of selection; (2) higher levels of selection are theoretically *possible* but improbable; and (3) genes are the fundamental "units of selection" because they are the basic units of replication. For the most part, group selectionists and individual selectionists both agree on the first and third points; higher-level adaptations must occur at higher levels of selection, and genes are the primary units of replication. Where the two camps diverge is on the second point – how *probable* was group selection in evolutionary history? W & S and other group-selection proponents believe that the probability of group selection was relatively higher than do advocates of individual selection. Thus, the debate mainly involves the issue of "likelihood," which, in turn, may depend on the species under consideration.

Some of the eusocial insects may have evolved in response to selection pressures at the group level (Seeley 1989). Indeed, haplodiploid reproduction in Hymenoptera (Hamilton 1964), which results in sisters sharing three-quarters of their genes instead of one-half, is a highly specialized adaptation that should increase genetic variation between groups (hives), thereby intensifying natural selection at the group level. The eusocial insects, however, are an evolutionary anomaly compared to most species alive today (Wilson 1971). W & S venture into deeper and more untested waters when they imply that selection at the group level might have occurred throughout the animal kingdom. Consider the case of mammals. During evolutionary history, some mammals (such as humans) probably did rely more heavily on coordinated groups to raise their young, hunt and gather food, and defend their territories. Other mammals – especially the more polygynous and solitary ones – probably did not and could not benefit as much from involvement in groups. Hence, even within a single class of species, group selection might have influenced the evolution of only some species. The group selectionist debate, therefore, may have to be conducted on a species-by-species basis.

W & S argue that individuals and groups can both serve as "vehicles" that carry genes and, consequently, as entities on which natural selection can operate. Yet there is a critical difference between individuals and groups as genetic carriers. Genes are effectively "trapped" within the individual; the individual's fitness is tied directly to whether or not genes replicate and are passed on to subsequent generations. However, genes are not necessarily "trapped" within groups, because individuals can migrate out of disadvantaged groups. Genes in individuals will usually maximize their own fitness if the individuals maximize their inclusive fitness, whereas the link between genes and groups is more tenuous. As a result, natural selection should have carved more effective and more precise adaptations by operating at the individual level (see Daly & Wilson 1983).

The strongest evidence that W & S marshall in support of group selection is presented in Figures 2 and 3. Figure 2 is particularly interesting because it reveals how altruism could be selected for at the group level. Unfortunately, W & S did not systematically vary the three parameters in their model: costs, benefits, and proportion of altruists in a group. Through varying these parameters, the conditions under which group selection for altruism could have evolved become more apparent. The most interesting and realistic sibling groups involve a mix of altruists (AA or Aa individuals) and nonaltruists (aa individuals). Using W & S's equations, I calculated the fitness of altruists (W_A), nonaltruists (W_S), and W & S's Group Fitness Index (GFI)

for mixed groups of $N = 10$ individuals with costs (c), benefits (b), and the proportion of altruists (p) set at three levels. Results are reported in Table 1.

Given how strong selection pressures ought to be at the individual level (Trivers 1971), W & S's model should be sensitive to some limiting conditions imposed by selection at this level. Group selection for altruism should not have evolved unless groups containing some altruists developed and remained *stable* over time. On average, altruists should not have remained in, or continued to contribute benefits to, groups that provided them with fitness values below those they could attain outside the group. Thus, when W_A dropped below 1, altruists should either have reduced their level of benefits to the group or left it entirely. Table 1 indicates that when costs, benefits, and the proportion of altruists are varied, W_A is greater than 1 in only a few of the scenarios reported. When costs are low ($c = .25$), benefits are high ($b = 1.0$), and when a group has many altruists ($p = .75$), the average fitness of altruists, nonaltruists, and the group are all high. However, as costs increase, benefits decline and the percentage of altruists declines, the fitness indexes for both altruists and the group plummet. These data suggest that

Table 1 (Simpson). *Fitnesses of altruists (W_A), nonaltruist (W_S), and groups (Group Fitness Index: GFI) when costs (c), benefits (b), and proportion of altruists in a group (p) vary*

Parameter values: Costs (c)/benefits (b)/ altruists in group (p):	Fitness indexes: W_A : W_S : GFI:
.25 / 1.0 / .75	1.47 1.83 15.62
.25 / 1.0 / .50	1.19 1.56 13.75
.25 / 1.0 / .25	.92 1.28 11.88
.25 / .75 / .75	1.29 1.63 13.75
.25 / .75 / .50	1.08 1.42 12.50
.25 / .75 / .25	.88 1.21 11.25
.25 / .50 / .75	1.11 1.42 11.88
.25 / .50 / .50	.97 1.28 11.25
.25 / .50 / .25	.83 1.14 10.63
.50 / 1.0 / .75	1.22 1.83 13.75
.50 / 1.0 / .50	.94 1.56 12.50
.50 / 1.0 / .25	.67 1.28 11.25
.50 / .75 / .75	1.04 1.63 11.88
.50 / .75 / .50	.83 1.42 11.25
.50 / .75 / .25	.63 1.21 10.63
.50 / .50 / .75	.86 1.42 10.00
.50 / .50 / .50	.72 1.28 10.00
.50 / .50 / .25	.58 1.14 10.00
.75 / 1.0 / .75	.97 1.83 11.88
.75 / 1.0 / .50	.69 1.56 11.25
.75 / 1.0 / .25	.42 1.28 10.63
.75 / .75 / .75	.79 1.63 10.00
.75 / .75 / .50	.58 1.42 10.00
.75 / .75 / .25	.38 1.21 10.00
.75 / .50 / .75	.61 1.42 8.13
.75 / .50 / .50	.47 1.28 8.75
.75 / .50 / .25	.33 1.14 9.38

Note: N = 10 individuals per group. Following Wilson and Sober, the equations used are as follows:

$$W_A = 1 - c + b(Np - 1)/(N - 1)$$

$$W_S = 1 + bNp/(N - 1)$$

$$GFI = (W_A Np) + (W_S (1 - Np))$$

for altruism to evolve via group selection a rather specific set of conditions must exist. The conditions entail relatively low costs, high benefits, and high proportions of altruists in groups.

Table 2 reveals how different levels of each parameter influence the three fitness indexes when fitness estimates across all levels of the other two parameters are averaged.

As the proportion of altruists in a group declines, the fitness indexes for altruists, nonaltruists, and the group all decline, with the relative drop in fitness being the same for altruists and nonaltruists (.21 fitness units each). Thus, everyone benefits from more altruists in a group. With increasing costs, fitness indexes for both altruist and the group decline, whereas nonaltruists are not affected. When benefits decrease, all three indexes decline, with slightly larger decrements experienced by nonaltruists (.14 fitness units) than altruists (.11 fitness units). Except for nonaltruists, the fitness indexes are highest when the ratio of costs to benefits is lowest (.25, in this set of equations). Across different levels of these parameters, then, the ratio of costs to benefits must be relatively low and the percentage of altruists must be relatively high for groups to remain stable enough to foster altruism at the group level.

Hamilton (1964) has proposed that altruism should not have evolved among individuals who shared one-half of their genes (e.g., siblings) unless the ratio of costs to benefits averaged less than .50. Table 2 shows that when the average ratio of costs to benefits is .50, W_A equals .96. This finding corroborates the supposition that the altruist fitness index must be at least 1 for altruism to evolve within either individuals or groups.

In sum, group selection for altruism is mathematically possible, but the conditions must be favorable. To strengthen their case for humans, proponents of group selection must provide evidence that these conducive conditions existed during evolutionary history and that human groups varied significantly in the fitness they conferred on their members.

Table 2 (Simpson). *Fitnesses of altruists (W_A), nonaltruists (W_S), and groups (Group Fitness Index: GFI) averaged across different levels of costs (c), Benefits (b), and proportion of altruists in a group (p)*

Parameter values:	Fitness indexes:		
	W_A :	W_S :	GFI:
p = .75	1.04	1.63	11.88
p = .50	.83	1.42	11.25
p = .25	.62	1.21	10.63
c = .25	1.08	1.42	12.50
c = .50	.83	1.42	11.25
c = .75	.58	1.42	10.00
b = 1.0	.94	1.56	12.50
b = .75	.83	1.42	11.25
b = .50	.72	1.28	10.00
c/b = .25	1.19	1.56	13.75
c/b = .33	1.08	1.42	12.50
c/b = .50	.96	1.42	11.88
c/b = .67	.83	1.42	11.25
c/b = .75	.69	1.56	11.25
c/b = 1.0	.65	1.35	10.00
c/b = 1.50	.47	1.28	8.75

Note: N = 10 individuals per group.

Semantics, theory, and methodological individualism in the group-selection controversy

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Abstract: Though it makes some useful contributions to the debate about group selection, the target article suffers from several important flaws: (1) conflating semantical, theoretical, and empirical issues; (2) distorting the contributions of Dawkins, Williams et al. to this debate; (3) conflating selection acting on groups with selection of group adaptations; (4) misconstruing the relationship between methodological individualism (MI) and self-interest; (5) exaggerating the extent to which MI dominates the human sciences; (6) glossing over some crucial differences between Hutterite collectivities and eusocial insect colonies; and (7) failing to advance the group-selection debate beyond primarily semantic issues.

Wilson & Sober's (W & S's) target article makes some positive contributions. In particular, I appreciate: (1) its clear and forceful statement of a hierarchical theory of natural selection; (2) the valuable warning against dogmatic denial of the possibility of group selection; and (3) the useful bibliography. By my evaluation, however, the problems far outweigh the benefits. To wit:

1. Conflating semantical, theoretical, and empirical issues.

The target article is replete with unsubstantiated empirical claims that are presented as deductions from a hierarchical theory of natural selection. For example: "group-level functional organization is not a 'byproduct' of self-interest in humans any more than it is in honeybees" (sect. 2); or "group selection is seldom the only force operating on a trait" (sect. 2.2). These are very sweeping claims, and each would take many research lifetimes to test. I return to this general issue below.

2. Distorting the contributions of the anti-group-selectionists.

Williams (1966, p. 92; cited by W & S) argued that "group-related adaptations do not, in fact exist" – an empirical claim. He also argued that the processes of genetic replication (via sexual reproduction) and gene flow (between populations or other groupings) made selection for individual adaptations a stronger force than selection for group adaptations – a theoretical claim that, if true, would explain the empirical claim. He did not proound what W & S misname "Williams's first commandment" (sect. 1.2), though arguably many who accepted his conclusions without understanding how he reached them might have been so dogmatic. This rhetorical move trivializes Williams's contribution to the history of biological thought, and the substance of his 1966 book.

Because W & S agree with Dawkins, Williams and others that only genes are plausible candidates for replicators in biological evolution, I think it unfortunate that they introduce or perpetuate semantic confusion by referring to those they criticize as "gene-centered." The term "anti-group selectionists," though cumbersome, would certainly be more accurate.

W & S rely crucially on the replicator-vehicle distinction, but they distort the history of this distinction, a distinction coined and theorized, after all, by Dawkins (1976; 1982a), a central architect of the "gene-centered" approach of which W & S are so disdainful. W & S agree with the anti-group selectionists that genes are the only reliable replicators in biological evolution. They agree that it is the "shared fate" of genes in individual reproduction that is responsible for the evolution of individuals (collections of genes, and the phenotypes they produce) and of individual adaptations. Dawkins and others have made considerable effort to explain why evolution acting on genetic replicators could lead to the evolution of individuals, as well as higher entities such as families, kin groups, and populations. To then argue (sect. 1.6) that so-called "gene-centered theorists now concede" that identification of the gene as the replicating unit in bioevolution is "irrelevant to the question of whether groups can

be like individuals in the harmony and coordination of their parts" is quite misleading, in two ways. First, it implies that the anti-group selectionists have "conceded" some important point in the debate that weakens their original position; I see no evidence that they have. Second, even the group-selection models discussed by W & S do not make the unit of replication "irrelevant" to identifying evolutionary vehicles, because the "shared fate" criterion requires that both replicator and vehicle be specified. This seems to be a clear case of rhetorical hyperbole on the part of W & S.

3. What Is group selection? To call evolved traits that favor certain forms of social interaction "group selection" simply because the existence of groups alters the fitness of the trait is to conflate selection acting on groups (and their individual members) with selection of group adaptations. As Maynard Smith puts it:

If [female-biased sex ratios] were a group adaptation, we would expect the sex ratio produced to be that which is optimal for the group, but it is not. For the group, the best sex ratio would be more female biased than it is. In fact, the sex ratio that evolves is the one that is optimal for the individual, in terms of the number of genes passed on to grandchildren. . . . The Hamilton ratio is the one that maximizes individual fitness: it does not maximize group fitness. (Maynard Smith 1987b, p. 148)

A blindness to this issue pervades the target article, particularly in the discussion of hypothetical examples and payoff matrices in section 1.6. The failure to resolve this issue after two decades of debate about the new group selection suggests to many of us that the debate is more about semantics or academic politics than it is about substance.

4. Conflating methodological individualism with the self-interest assumption. W & S assert (sect. 2.2 & 2.4) that the human behavioral sciences are "dominated" by methodological individualism (MI) to such an extent that opponents of "psychological selfishness" are "an embattled minority who must constantly defend themselves against a monolithic individualistic world view." I believe their position embodies several serious errors.

First, it does not correspond to contemporary or historical academic realities. In one or two fields (economics and [parts of] psychology) MI is surely dominant; but just the opposite is true in the majority of social science disciplines. And this has been the case throughout the history of the social sciences. In socio-cultural anthropology, from Boasian cultural relativism to "personality and culture" studies in which entire social systems had "Apollonian" or "Dionysian" styles, on to structuralism, neo-Marxism, functionalist ecology, and the current theorizing in which Foucauldian systems of power/knowledge unfold in history, MI is truly the embattled minority position. A similar account could be given for sociology, political science, and history, where a focus on institutions, class interests, gender, ethnic groups, and nation-states is dominant.

Second, W & S have conflated MI with the assumption that individuals are driven by self-interest. But MI per se does not entail an assumption of selfishness or self-interest. Put as simply as possible, MI asserts that the properties of any group result from the actions and interactions of its individual members (Elster 1983; Smith & Winterhalder 1992); this can remain true even if these individuals are altruistic, dedicated to the collective good, and so on.

Third, Campbell's (1993) equation of MI with a denial of the ontological status of groups (cited in sect. 2.2) is an example of the polemical hyperbole to which some opponents of MI resort; in my experience, practicing social scientists (as distinct from philosophers) hardly ever engage in ontological debates about groups, and adherents to MI rarely deny the "reality" of collectivities. Rather, they deny that such collectivities have agency, and they insist on "microfoundations" for all explanations of social and historical process, that is, explanations that proceed

from individual actions (including the historical residues of past actions).

In defense of MI, I would urge extreme skepticism of phrasing or theory that attributes agency to collectivities (as in the claim that "the hive responds . . . by shifting workers" [sect. 1.4.2] or the discussion of "group-level cognition" in human groups [sect. 2.5]). Not only do such moves impute consciousness and intentionality to entities where such has never been demonstrated, but they mask the potential for individual members of such collectivities to have conflicting understandings or intentions and to perform actions at cross purposes. Even where individual actions and intentions are coordinated to achieve a collective outcome, there is no justification for attributing agency to the collectivity, as if it had eyes that see and hands that move. Finally, such collective coordination is not evidence in itself of a history of group selection, a point I believe the target article recognizes in principle but to which it does not always adhere.

5. The Hutterite case. I will leave evaluation of the Hutterite analysis to others more familiar with it. In general, I found myself relatively sympathetic to the discussion in this section (2.6) of the target article. I do have two criticisms, however. First, W & S do not include the hypothesis of cultural group selection (e.g., Boyd & Richerson 1982; 1985) in their list of alternative explanations, perhaps because it does not fit neatly into their dichotomy between self-interest and group-interest. Second, the social-insect analogy is crucially flawed in that all Hutterites are expected to marry and raise as many children as possible; there are no sterile castes (and where these have arisen in *human* social systems, generally strong coercion has been required). This is a critical point, in that it is the *reproductive* division of labor that makes group selection a strong contender for explaining social insect colonies.

6. Where's the beef? There is much conceptual agreement between so-called gene-centered theorists and the target article: only genes make good replicators (in biological evolution). Vehicles are sets of genes that have a shared fate; selection creates adaptations at the level of vehicles. So what substantive contribution does the new group-selectionism bring to orthodox evolutionary biology? If groups (other than small groups of close kin) are often vehicles, we should expect to be able to find many group adaptations, that is, features of groups that evolved to maximize group fitness. The theoretical work of Hamilton, Williams, and Trivers has inspired a truly monumental array of empirical evidence on individual and kin-group adaptations, running to tens of thousands of publications. The new group selectionists have been propounding their views since the early 1970s; where is the empirical evidence for the widespread occurrence of group-level adaptations in nature? My reading of the literature is that the evidence to date is very thin. Much effort has gone into scholastic arguments about whether the evolutionary dynamics of kin interactions first theorized by Hamilton (i.e., "kin selection") are examples of gene-level selection or group selection. If trait-group selection models make no predictions not made by classical kin selection and evolutionary game theory, then perhaps this is not a very fruitful debate. In this war of words, I am still waiting for the empirical payoff.

Empirically, the orthodoxy that individuals, dyads, or small groups of close kin are often vehicles, whereas higher-level entities are usually not, seems well supported to date. Theoretically, the reasons seem to be essentially those first identified by Maynard Smith (1964), Williams (1966), and Dawkins (1976). In particular, the *rate* of evolution is generally higher for individual adaptations than for higher-level ones; and the *shared fate constraint* is generally stronger for genes in individuals than for genes in higher-level vehicles. I do not believe these generalizations should become dogma (as I realize they have for some), but in turn I do not believe the target article provides significant reasons for concluding that they are in error and should be discarded.

Vehicles all the way down?

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

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

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

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

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The maintenance of behavioral diversity in human societies

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

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

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

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

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

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

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

generation in such a system, but far fewer than if the host population consisted of only one genotype, which would allow one pathogen to multiply unchecked and perhaps drive the host population to extinction.

My guess is that something like this may be operating in human societies, but with changes in behavior that depend on the frequencies of other behaviors. The group-selection models presented by W & S assume that the behavioral types in each population either do not alter their behaviors or alter them only under certain precisely specified conditions. There is no feedback, though we certainly know that such feedback is plentiful in human societies. The spread of a particular behavioral pattern in a human society (all those greedy "Gordon Geckos" of the 1980s, for instance) eventually makes things so unbearable for the majority (the rise of homelessness, the increase in crimes committed by the angry disadvantaged) that the behaviors of many members of society change slightly and as a result we move into the "Caring '90s." No appreciable genetic change has happened in American society in the last 10 years, but there has been a slight societal correction that gives an advantage (alas, certainly a temporary one) to less selfish behaviors.

In the MHC model we have proposed, there is a premium put on genetic diversity. If the MHC alleles are very different from each other (and they are, by the way; two alleles in the same population may differ by as many as 20 amino acids), then no single pathogen will be sufficiently versatile to be able to attack carriers of the various alleles with equal effectiveness. It may not be unreasonable to suppose that the same thing applies to human behaviors: psychologists dealing with perception and behavior have documented immense diversity in our species, at least some of which must have a genetic underpinning. We must add to the model the assumption that there are temporary reproductive advantages to people exhibiting certain behaviors, advantages that disappear when these behaviors become too common.

Much has been made of group selection and altruism. Obvious altruistic behavior is rare in human societies, but if there are genes that contribute to altruistic behavior, we must all carry some of them. They need not be maintained by blatant self-sacrifice; all that is required is a slight shift in the norms of society, something that is happening all the time. I do not deny the existence of group selection – it has probably had much to do with the maintenance of sexual reproduction, for instance – but I feel much happier about a model that explains the majority of the diversity of human behavior on the basis of individual selection. It is so much more effective.

Authors' Response

Group selection: The theory replaces the bogey man

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Abstract: The largely receptive comments on our target article suggests that group selection will be treated as a viable hypothesis in future discussions of human evolutionary biology. Our response focuses on: (1) the concept of heritability and fitness at the group level; (2) clarifying the vehicle concept; (3) empirical evidence for group selection; (4) genes as replicators; (5) pluralism and the sense in which group selection theory is compatible with the gene-centered approach; (6) additive versus nonaddi-

tive interactions; (7) the relationship between group selection, frequency dependent selection, and Sober's earlier argument based on causality; (8) the relationship between evolutionary and psychological definitions of selfishness; (9) egalitarian social organizations in ancestral environments; (10) culture and group selection; (11) group selection and the adaptationist program; and (12) criteria for evaluating group selection theory.

One of our goals was to replace the bogeyman version of group selection with the actual theory that has developed over the last twenty years. The largely receptive response to our target article suggests that we have accomplished this goal and that group selection will be treated as a viable hypothesis in future discussions of evolution and human behavior.

Our reply will follow the organization of the target article, dealing first with biological issues and then with implications for the human behavioral sciences.

R1. Biological issues

R1.1. Natural selection as a process that operates on a hierarchy of units. Questions about the concepts of heritability and fitness at the group level are raised by Alroy & Levine and Holsinger. Holsinger seems to confuse heritability with the replicator concept when he states that groups must be replicators in addition to vehicles. Individuals are not replicators, even though traits are heritable at the individual level, and the same can be said for groups. Empirically, heritability at the individual level is measured as a correlation between genetic relatives or as a response to selection in artificial selection experiments (Falconer 1981). If genetic effects are made explicit in a population genetics model, the breeding value of a genotype can be calculated as the sum of the average effects of its component alleles and narrow-sense heritability can be calculated as the ratio of the variance in breeding value to the total phenotypic variance. Variation in breeding values requires variation in average effects, which is in turn required for natural selection to occur. Thus, fitness is heritable at the individual level whenever natural selection occurs in a standard population genetics model.

Because two-person game theory is mathematically identical to a diploid single-locus model, with individuals in groups instead of genes in individuals, it would be strange indeed if the associated concepts of average effects, breeding values, parent-offspring correlations, and narrow-sense heritability could not be frameshifted upward (*contra Alroy & Levine*). To begin with the simplest case, assume that A1 and A2 are asexual types and that the payoff matrix in Figure 4a gives the number of offspring produced as the result of each interaction. We can identify three "group-types" (A1A1, A1A2, and A2A2) that are the exact analog of genotypes. Group fitness can be defined as the total number of offspring produced by the interaction (WA1A1 = 10, WA1A2 = 8, and WA2A2 = 6). This definition is straightforward and considerably less abstract than the definition of inclusive fitness, which involves the reproduction of multiple individuals weighted by the coefficient of relatedness with the actor. As we mentioned in section 1.6 (para. 10), the average fitness of A1 and A2 is exactly analogous to the average effects of alleles. The individuals in any group can be traced to two parental groups, just as genes in an individual can be

traced to two parents. The progeny that emerge from A1A1 group-types will randomly enter groups of their own. As A1 individuals, however, they can exist only in A1A1 or A1A2 group-types, in contrast to the progeny of A1A2 and A2A2 groups. This means that the fitness of offspring groups will be correlated with the fitness of parent groups, exactly as in a population genetics model and contrary to Holsinger's claim that parent-offspring correlations do not exist in randomly formed groups. Without belaboring the point, the entire apparatus can be frameshifted upward, including the calculation of breeding values and narrow-sense heritability (Wilson & Sober 1989). That is the beauty of the hierarchical approach.

As we depart from the simplest case of two-person game theory, the details change but the fundamentals do not. For $N > 2$ we can still identify an array of group-types and trace parent-offspring relationships, although each group now has N parents. As N increases, the difference between average effects at the individual level and resulting narrow-sense heritability at the group level declines, but this merely restates the well-known fact that group selection requires genetic variation among groups, which is inversely related to N . If we model nonrandom group formation (i.e., kin selection), group-level parent-offspring correlations and narrow-sense heritability increase along with genetic variation among groups, as they must, because they are all different ways of expressing the same thing.

The hierarchical theory makes it obvious that natural selection at all levels requires variation, random or otherwise. Kin selection enters group selection theory in exactly the same way that inbreeding enters population genetics theory: as a factor that increases genetic variation among groups/individuals but is not required for group/individual selection to take place. It follows that group-level adaptations can evolve in randomly composed groups when selection within groups is sufficiently weak or selection among groups is sufficiently strong (Wilson 1990). The same expectation does not emerge from inclusive fitness theory, which makes relatedness appear to be a necessary requirement for group-level adaptation. This is a good example of the simple but foundational changes that take place when evolutionary theory is restructured around the vehicle concept.

R1.2. Clarifying the vehicle concept. Many questions were raised about the concept of vehicles and in retrospect, we see how our target article may have contributed to some of the confusion. We agree with Grantham that it is important to distinguish between the *process* of group selection, which is based on where fitness differences occur in the biological hierarchy, and the *product* of group selection, which is group-level adaptation. No one would be interested in group selection if it *never* resulted in group-level adaptation, so in this sense the debate is indeed centered on whether groups can be like organisms in their functional organization. As Grantham notes, however, the process of group selection should be defined independently of its product. Group selection can occur even when it does not result in group-level adaptations, such as when it is opposed by strong individual selection. (Goodnight's statistical methodology makes this clear.)

The distinction between process and product can be

used to clarify some of the other comments about vehicles. Several authors implied that groups are not vehicles of selection because fitness differences are not concentrated *entirely* at the group level (Bradie, Cronk, Dennett, Heschl; but not MacDonald, Miller, or Simpson). This is not true and we never meant to imply it. It is true that when fitness differences are concentrated entirely at the group level, the group becomes an organism in every sense of the word. As we depart from this ideal, the traits that evolve reflect a conflict between levels of selection. The group loses some of its organic properties but this does not mean that group selection has ceased to operate; it merely is no longer the *only* force that operates. Altruism can evolve by group selection even though it is opposed by individual selection.

The same distinctions can be made at the individual level. Dawkins (1989) states that "the essential quality for an effective gene vehicle is an 'impartial exit channel into the future, for all genes inside it.'" Perhaps, but impartial exit channels such as the rules of meiosis are the *product* of natural selection and should not be used to define the process. The *process* of individual-level selection is defined by fitness differences among individuals within groups, which presumably existed before (and were responsible for) the evolution of elaborate adaptations such as the rules of meiosis. The rules of meiosis perfect the individual as a vehicle of selection by reducing intragenomic conflict, but they do not define the individual as a vehicle of selection. Similarly, when the rules of meiosis are broken by "outlaw" genes, we do not say that the among-individuals selection ceases to operate, only that it is opposed by among-gene selection within individuals.

Against this background, we think that Dennett's critical comments lose much of their force. Dennett emphasizes the fact that cells within a multicellular organism have a common ancestry, whereas the numerous parasites and microbes that share the same body do not (see also Nesse). However, common ancestry per se is not relevant to the evolution of functional organization. The genetic elements that make up a single cell do not have a common ancestry in sexually reproducing organisms, but this does not prevent them from interacting harmoniously. In addition, if cells within a multicellular organism become genetically diverse by mutation, the problems of within-individual selection arise even though all cells are derived from a common ancestor. Indeed, Buss's (1987) interpretation of development suggests that competition among cell lineages within an organism must be carefully managed despite the fact that they are all derived from a single egg. Parasites evolve to act entirely in the interests of their hosts if parasite transmission is entirely vertical (offspring transmitted only to host offspring). The prerequisite for functional organization in all of these examples is shared fate, regardless of common ancestry. Dennett's main point is that natural selection is concentrated almost entirely at the individual level for genes/cells in an organism but only partially at the group level for parasites in hosts and human individuals in groups. We agree, and tried to emphasize the same point ourselves. We hope Dennett will agree that group selection can be a *significant* force even when it is not the *only* force. Furthermore, the balance between levels of selection varies widely on a trait-by-trait basis and examples can be found

in which group selection is the predominant force in both parasite and human groups. As a technical aside, group selection in parasites should not be equated with mutualism between the parasites and the host, because parasites can also cooperate with each other to subvert the host (e.g., Wilson 1977b).

We are fortunate to have both Hull and Dawkins comment on our use of the vehicle concept. Hull basically agrees with our position, but points out differences between his own concept of interactors and Dawkins's concept of vehicles, which we treat as the same. Our usage is closer to Hull's, because it is based on fitness differences and not on development *per se*. Thus, genes can be vehicles (as we use the term) in addition to replicators and it is hard to think of cases of intragenomic conflict in any other way. However, it seems to us that Dawkins's use of the term vehicle is based on fitness differences in addition to development (cf., the rowing crew metaphor), so he may not agree with Hull's characterization.

Dawkins remains so near, yet so far. He cannot see the cricket pair as a vehicle of selection, despite the fact that we deliberately fashioned the example after his own rowing crew metaphor. He says:

There is no vehicle of selection in this case. It is a terrific vehicle-undermining example. Natural selection favours replicators that prosper in the environment. The environment of a replicator includes the outside world, but it also includes, most importantly, other replicators, other genes in the same organism and in different organisms, and their phenotypic products. Cricket genes, for cooperating in the presence of another cooperating cricket, prosper. This statement is true and illuminating, in precisely the same sense as the statement that genes for thick, hairy coats prosper in the presence of snow. Like snow, each cricket is part of the environment of the other one's genes.

We could not ask for a better summary of the gene-centered view. The question is, are vehicles of selection absent from this account or have they merely been reconceptualized as environments of the genes? The answer to this question is obvious at the individual level, because Dawkins acknowledged long ago that individuals can be vehicles of selection, (and therefore organisms) despite the fact that they are also environments of the genes. The answer is just as obvious at the group level in our cricket example, although Dawkins may decline to acknowledge it. This passage does not refute the existence of vehicles, but merely assumes that the vehicle concept can be dispensed with and that natural selection can be studied entirely in terms of average genic effects. Yet, in the very same commentary, Dawkins states that "the group-selection controversy ought to be a controversy about groups as vehicles." We hope that the reader can see the contradiction even if Dawkins cannot.

The example of figs and fig wasps that Dawkins intends as a challenge is nothing of the sort. He seems to think it is comparable to our cricket example, but it cannot be accommodated within a game theory framework because there are no such things as fig-fig and wasp-wasp groups. Wasps cannot replace figs in the population in the same way that cricket types can replace each other in our example. More generally, the sense in which highly co-evolved predators and prey share the same fate as species is completely different than the sense in which genes in an

individual vehicle or individuals in a group vehicle share the same fate. See Goodnight (1990a; 1990b), Wilson (1976; 1980; 1992a) and Wilson and Knollenberg (1987) for examples in which multispecies communities can be properly viewed as vehicles of selection.

R1.3. Empirical evidence for group selection. "Where is the empirical evidence for group selection?" Smith and Nesse ask. One answer is "female-biased sex ratios," which we mentioned briefly in section 1.4 (para. 7) and Note 11, but Smith and Nesse are unconvinced. We must therefore review the extraordinary history of this subject in more detail: (1) Williams (1966) used sex ratio as his best empirical test of group selection theory. He argued that group selection should favor a female-biased sex ratio to maximize the productivity of the group. Natural selection within groups should favor an equal investment in each sex as predicted by Fisher's sex ratio argument. Williams was unaware of any examples of female-biased sex ratios and concluded that no evidence existed for group selection. He was so impressed with his test that in the concluding section of this book (p. 272) he stated, "I would regard the problem of sex ratio as solved". (2) One year later, Hamilton (1967) reviewed many empirical examples of female-biased sex ratios and proposed a theoretical model to explain their evolution. There can be no doubt about the metapopulation structure of Hamilton's model (*italics in original*):

Free-moving females search for isolated food objects, or "hosts." Each host is colonized by a certain number and is eventually exhausted through feeding of the progenies. The subpopulation of adults reared on a host mates randomly *within itself*; no males successfully mate outside their own group. Inseminated females emigrate to take part in population-wide competition to discover new hosts.

Nevertheless, Hamilton did not compare fitnesses within single groups but used a game-theoretic approach that averaged fitness across groups. (3) The study of female-biased sex ratios became a hot topic in evolutionary biology at the same time that group selection entered its dark age. The theory was elaborated and dozens of new empirical examples were discovered. (4) Colwell (1981) showed that the assumptions of Hamilton's model conform exactly to Williams's original test for group selection. In other words, female-biased sex ratio alleles decline in frequency within groups and evolve only because they increase the productivity of the group. The so-called optimal sex ratio is in fact an equilibrium sex ratio that reflects the balance between levels of selection. The equilibrium is influenced by a number of factors, some that were included in Hamilton's model (e.g., number of individuals colonizing the group) and some that were not (e.g., population regulation within groups prior to dispersal). Thus, the group selection model of sex ratio both reinterprets the original model and makes predictions that were not forthcoming from the original model. (5) Charnov (1982) and other authorities on sex ratio quickly accepted Colwell's interpretation but Maynard Smith (1987a; 1987b) and others staunchly maintained that group selection is absent from Hamilton's model. The Maynard Smith passage quoted by E. A. Smith contains two errors that become obvious when we take vehicles seriously. First, the sex ratio that maximizes group fitness is not expected to evolve unless group selection is the only

evolutionary force. The beauty of sex ratio is that it measures the relative intensity of within- versus between-group selection. Any deviation in the direction of female bias that evolves for the reasons identified by Hamilton's model demonstrates that group selection is a measurable force. Second, if the term "individual fitness" means relative fitness within groups, it is the Fisher ratio, and not the Hamiltonian ratio, that maximizes individual fitness.

Recently, Williams (1992, p. 49) himself has acknowledged that female-biased sex ratios constitute empirical evidence for group selection: "I think it desirable, in thinking about organisms for which the haystack model is descriptive, to realize that selection in female-biased Mendelian populations favors males, and that it is only the selection among such groups that can favor the female bias." Perhaps we can look forward to general agreement in the future, but the entire episode can be used to make a more general statement. Just as group selection can be made to disappear from a theoretical model by averaging the fitness of individuals across groups, so also can it be made to disappear from empirical studies. As soon as we take vehicles seriously by comparing fitness within single groups, group selection becomes an empirically well supported theory, not only for sex ratio but for many other traits (see Table 1 entries marked with an "E"). It is exasperating to have Smith accuse us of blindness on the matter of sex ratios and then innocently ask "where's the data?"

R1.4. Genes as replicators. In our target article we concentrated on showing that the replicator concept is irrelevant to the group selection controversy. Griffiths & Gray and Thompson are sympathetic to this conclusion but also want to criticize the replicator concept itself. We agree that genes no more replicate themselves than do the pages fed into a photocopier. Genes (pages) get replicated, but to say that they are replicators is to mischaracterize the causal process.

Thompson asks whether there is any point in retaining the replicator concept. Although we think that this concept needs some fine-tuning, we still think it answers a fundamental question concerning the unit of heredity (see also Crow). When offspring resemble their parents, and do so for reasons not attributable to shared environment, we attribute this resemblance to genes. The idea that there must be a physical mechanism that mediates this parent-offspring resemblance is what leads to the idea that there must be one or more "units of heredity." Genes subserve this function; this is the privileged status they have in evolutionary processes. In saying this, one leaves open the characteristics of the mapping between genes and phenotypes. How large a strand of DNA must one consider before it becomes sensible to describe the phenotypic effect of that strand? This is the empirical issue that Dawkins was thinking about when he reflected on the longer but more accurate title for *The selfish gene* to which Thompson refers. Dawkins recognized that there is a trade-off between the longevity of a strand and its phenotypic power. This is an important point, but it does not undermine the idea that genes are units of heredity.

R1.5. On pluralism. In the form of pluralism Holcomb advocates, group selection theory and "broad-based individual selection" are observationally equivalent. We think

a legitimate form of pluralism exists but that it does not extend to substantive empirical questions such as the nature of organisms or whether groups can be like organisms (Wilson & Sober 1989). For example, Dawkins's (1982a) necker cube metaphor implies that the gene's-eye view and the individual's-eye view are equivalent ways of looking at adaptations. This is not true for all adaptations, however, because there is no way to interpret meiotic drive and other forms of intragenomic conflict as adaptations at the individual level. In addition, the gene's-eye view cannot deny the fact that individuals are organisms (when they are vehicles of selection) without being just plain wrong. There is no room for pluralism on these substantive empirical issues. We are basically advocating that a group-level face be added to the necker cube. Group-level adaptations can be represented at the individual and gene levels by averaging the fitness of lower level units across higher level units. Gene- and individual-level adaptations cannot be interpreted as group adaptations without committing the errors of naive group selection, but the gene's-eye view and the individual's-eye view cannot deny the existence of group-level adaptations (when groups are vehicles of selection) without being just plain wrong. Thus, despite a weak form of pluralism, the answers to the most substantive questions are not just a matter of how you look at things. The reason we use the term "vehicle" in our target article, rather than the term "unit" as it is unambiguously defined within the group selection literature, is to force gene-centered theorists (or broad-based individual selectionists, to use Holcomb's term) to realize the logical consequences of their own framework.

R1.6. Additive versus nonadditive interactions. We have reviewed the philosophical literature on levels of selection elsewhere (Sober & Wilson 1994) but will comment here on the additivity criterion proposed by Wimsatt (1980) and Lloyd (1988), as requested by Hull. Basing his ideas on the holistic concept that "the whole is more than the sum of its parts," Wimsatt suggested that levels of selection can be defined on the basis of nonadditive interactions among genes in individuals or individuals in groups. Although this suggestion has been taken up by Lloyd and several other authors, it fails to capture even the most basic elements of the group selection controversy. For example, altruists have a purely additive effect on group fitness in the standard group selection model for the evolution of altruism. The additivity criterion would deny that the group is a unit of selection in this case. Furthermore, according to the additivity criterion, heterozygote intermediacy would count as an example of gene-level selection and dominance would count as an example of individual-level selection, even though adaptations that are good for the individual will evolve in both cases. It is true that any organism worthy of the name will have elements that interact nonadditively (as stressed by Griffiths & Gray, Heschl), but these do not define the process of group selection. We therefore cannot agree with Lloyd that our framework is similar to hers, at least in this respect.

R1.7. Group selection and causality. Several authors have raised questions about the relation of the target article to the causal characterization of the units-of-selection prob-

lem in Sober (1984). Contrary to what Alroy & Levine, Smith, and Wills have said, we have not defined group selection so broadly that it includes all forms of frequency dependence; the proposal in Sober (1984) was deliberately set up to avoid this consequence. For example, Wills describes a scenario in which genetic diversity is maintained by selection against common genotypes. This scenario does not invoke group selection because it can take place within a single group and does not require a metapopulation structure at all. We cite Wills (1991) in Table 1 for his interesting suggestion (pp. 213–14) that group selection has influenced the maintenance of genetic polymorphisms at the major histocompatibility complex (MHC) region and not for the more general scenario about frequency-dependent selection that he develops in his commentary. More generally, the need to invoke group selection can quickly be determined by asking whether a metapopulation structure is required for the trait to evolve.

Alroy & Levine go on to suggest that our talk of shared fate and of fitness differences at various levels constitutes two quite independent conceptions of the units-of-selection problem. We disagree. The individuals in a group have shared fate only if the survival and reproduction of some depends on the survival and reproduction of the others. Shared fate is a causal concept in which the relevant effects have to do with fitness. And, as our procedure makes clear, it is essential that there be variation in fitness at a level if there is to be selection at that level. As a result, Alroy and Levine's putative counterexample to our idea – that objects at all levels in the earth's ecosystem have the same fitness – does not work.

Bradie thinks that our characterization of the units-of-selection problem in terms of the idea of "common fate" ignores the distinction between "selection of" and "selection for" (Sober 1984). Although we grant that the idea of common fate requires more elaboration than space permitted us to provide, we believe that this is not a serious problem. If individuals in the same group are "in the same boat," this is because there is some common influence on them or interaction among them that has this fitness consequence. This is where the idea of "selection for" finds its application.

The criterion for discerning group selection given in Sober (1984) is, we believe, consistent with the formulation defended here. However, Sober's application of that criterion contained an inconsistency. As we have argued in the present article, it is important to treat the relation of genes to organisms in the same way one treats the relation of organisms to groups. Sober (1984) follows the shared fate idea when it comes to thinking about group versus individual selection but gets muddled when the issue of genic versus individual selection is considered (Walton 1991).

As we mentioned in Note 2, our target article reviews group selection at a very elementary level. Many of the issues raised by the commentators have been treated in detail by other authors or by us in other papers. We hope the reader will make use of Table 1 to become familiar with the primary literature.

R2. Group selection and human behavior

We are delighted that a number of commentators not only accepted the vehicle-based framework (Burghardt, Cloak, Dupré, Dugatkin, Frank, Gilbert, Grantham, Hyland, MacDonald, Miller, Rapoport, Thompson) but also used it to make points that we wish we had discussed in our target article. Dugatkin shows how cultural transmission of information about cheaters can alter the balance between levels of selection. Miller stresses that some forms of competition within groups can also be advantageous at the group level (see also our Note 24). In addition, the equalization of fitness within groups can take the form of a lottery, in which case the extreme difference in outcomes between winners and losers does not signify extreme within-group selection. This is similar to the "lottery" that causes some cells to enter the germ line and others to enter the somatic line (Buss 1987). Similarly, the comparison between group-level rules of meiosis and the veil of ignorance in Rawls's (1971) theory of justice (Dennett, Miller) is fascinating and should be developed. The connection between group selection and sexual selection made by Miller and MacDonald is important and should be explored for nonhuman species in addition to humans. We agree with Gilbert and Hyland that the psychology behind group-level adaptations in humans involves more than "altruism" as usually construed. Brace, Campbell & Gatewood, and Moore were skeptical about some aspects of the framework but also made valuable points about human groups as potential vehicles of selection.

R2.1. Evolutionary and psychological selfishness.

The following passage from Cronk shows that a very basic issue has not yet been fully resolved:

W & S choose the Hutterites to demonstrate that group selection has been important in the environments of human evolutionary adaptedness. In fact, the Hutterite example does just the opposite. In the first place, there is nothing very "selfless" about going along with a system that virtually guarantees you several times the reproductive success you could enjoy outside the system.

Cronk does not regard the Hutterites as selfless because they are more successful (reproductively) than non-Hutterites (see also Frank, Moore). We regard the Hutterites as selfless because they achieve their success by benefitting a collective, of which they are a part. Cronk does not compare fitness differences within groups and therefore ignores the concept of vehicles that forms the basis of our entire target article. Our purpose is not to castigate Cronk, however, but rather to discuss why the view he represents is so tenacious.

When a trait evolves by causing the gene to benefit the genotype it belongs to, it is easily classified as an example of individual selection. When a trait evolves by causing the individual to benefit the group it belongs to, any model that treats group selection as a process analogous to individual selection will classify it as an example of group selection, yet there is great reluctance to accept this view. We think the reluctance can be traced to a dissonance between evolutionary and psychological definitions of selfishness. Superficially, everyone familiar with the subject knows that evolutionary definitions are based on fitness effects, whereas psychological definitions are

based on the motives of the actor (**Batson**). Nevertheless, there is a deeply held assumption that the two definitions will roughly correspond to each other. In other words, what counts as selfish in an evolutionary model is assumed to correspond to what a psychological egoist interested only in his own reproductive success would decide to do in the same situation. This assumption is violated by the Hutterite example, because a psychological egoist would evaluate the options and decide to be a Hutterite. It therefore seems strange to call the Hutterites selfless in an evolutionary model.

One way to resolve the dissonance is by changing the definition of group selection (e.g., Nunney 1985b), but this destroys the analogy between group and individual selection. Alternatively, we can retain the theory of group selection as a process analogous to individual selection and accept the dissonance between evolutionary and psychological definitions of selfishness. After all, they are based on completely different criteria and perhaps we were naive to expect otherwise. A relationship between the definitions presumably exists, but it might be more complex than a one-to-one matching between traits that evolve and the decisions that a psychological egoist would make in a similar situation. For example, why should humans care about motives as long as the people they interact with are being nice to them at the moment? The obvious answer is that knowledge of motives helps predict how others will behave in the future and in different situations. A selfishly motivated person may be nice now but is likely to change; an altruistically motivated person will remain nice across most situations. Thus, even though psychological definitions appear to be based on motives, in a more subtle way their significance depends on long-term effects. Furthermore, the relationship between motives and effects is not a one-to-one correspondence (selfish people are not nasty all the time) but rather a more general correspondence when effects are averaged over many situations. If we replace the term "being nice to others" with "increasing the fitness of others," we have a relationship between evolutionary and psychological definitions of selfishness that is complex, rather than a one-to-one matching of behaviors with motives. We think that a *really* selfish motivated personality, who tried to maximize relative fitness within groups in all situations, would have gone extinct long ago. The personality we call selfish is in fact a flexible strategy that includes evolutionary altruism in its repertoire but is sufficiently prone to exploit others within groups that it cannot be trusted by a person trying to predict future behavior (Frank 1988). More generally, we think it is important to preserve the analogy between group selection and individual selection as mechanistic processes. If the products of within-group selection do not correspond to the decisions of a psychological egoist, that is something to be explored rather than avoided.

So far, we have argued that the social behavior of the Hutterites can be a group-level adaptation even if a psychological egoist decided to be a Hutterite. The question of what actually motivates people such as the Hutterites is a separate issue (e.g., **Cronk, Frank**). Consider a psychological egoist and a psychological altruist within a Hutterite society. Even though the egoist has decided to be a Hutterite because it is his best option, it does not follow that he will fare better than the altruist. For the

many decisions that must be made on a daily basis, if the adaptive choice is almost always to benefit the group, then a direct calculus of group interest will arrive at this choice faster and with fewer errors than a more tortured calculus based on self-interest. It is simply more efficient to be an altruist. Thus, communal social organizations can provide an environment that selects for psychological altruism, not only culturally but biologically (**Campbell & Gatewood**). The Hutterites are not necessarily selfish just because a selfish person would decide to become a Hutterite.

Campbell & Gatewood think the biggest challenge for group selection theory is to explain suicidally altruistic behavior on behalf of groups that are not composed of close kin. This is indeed a challenge but we think it is peripheral to the main enterprise of studying group-level adaptations in all of their forms, altruistic and otherwise. For example, the social convention of drawing straws is so mundane that no one bothers to think about it, but it becomes interesting when we examine its effects on fitness differences within and between groups. It begins with a situation in which an individual must sacrifice his welfare to benefit the group. Such behaviors are regarded as altruistic when performed voluntarily and are usually thought to evolve only when the group is composed of kin. However, the social convention of drawing straws allows the same behaviors to be performed among non-kin. Because the "altruist" is chosen by a lottery process, the costs and benefits of altruism are equally shared in a probabilistic sense, eliminating fitness differences within groups (**Miller**). We no longer call the behavior "altruistic" in a psychological sense, but we should still recognize it as a group-level adaptation because groups that draw straws succeed as a collective, relative to groups that do not. In fact, drawing straws should be successful whenever the benefits for the recipients exceed the cost for the donor, whereas voluntary sacrifice toward relatives must be discounted by the coefficient of relatedness. Interactions among unrelated individuals who draw straws should therefore be *more* "altruistic" than voluntary interactions among genetic relatives!

As it turns out, unrelated individuals in close-knit social groups often do not draw straws but vie with each other to be altruistic in situations that require personal sacrifice. Evidently there are other social conventions that are even better at promoting sacrificial behavior among nonrelatives than drawing straws. However, in addition to studying these social conventions (**Campbell & Gatewood's** challenge), we must also learn to see mundane social conventions such as drawing straws in a new light.

R2.2. Ancestral environments: Some commentators (**Cronk**) but not others (**Hyland, Moore**) dispute our claim that egalitarian social conventions similar to those of the Hutterites exist in tribal societies. This is such an important subject that we will provide an example from Boehm (1994) that shows how decision making in tribal societies can be a group-level process in which fitness consequences within groups are carefully regulated. Boehm is quoting from Meggitt's (1977) monograph on Mae Enga raiding and warfare in Highland New Guinea.

Meggitt (1977) explains that it is only the men who meet, very quietly; anyone who has passed through the bachelor's asso-

ciation is eligible, and it is taken for granted that everyone will choose to participate. Pooling of information is important:

The men who initiated the conference, or their spokesman, briefly indicate their view of the clan's position and the action they favor. Thus, they may argue that now is the time to launch a full-scale attack on the neighboring clan with the aim of occupying a specific section of its territory. The major Big Man then solicits responses from the audience. Ideally, everyone present has a voice and, being among his own clansmen, can speak with complete freedom. Moreover, anyone who possesses pertinent information has a moral obligation to contribute so that the group may reach the best possible decision in the circumstances. Most men . . . are ready to make their points at length and with elaborate oratorical flourishes . . . The task of the Big Man at this stage is to insure that all have a chance to offer their opinions and facts in full, and . . . [to make] no attempt to cut off any but obviously irrelevant speeches.

Only in this way, it is believed, can each clansman truly ascertain the thoughts of his fellows and the evidence behind them. So instructed, he can cling to or modify his own ideas, and his reactions in turn affect those of others. Naturally, the Big Men and fight leaders have their own opinions of an appropriate outcome of the discussion; but none of them, especially in the early sessions, reveals much of his hand or tries patently to push for the acceptance of his suggestions. Not until hours of argument have clarified the issues and carefully dissected the facts are these men likely to signal unequivocally their own positions, and even then those, including the major Big Man, who perceive the tide running strongly against them may well go along with the emerging majority view. Thus, step by step the slow process of constant feedback inches toward the possibility of general agreement on a correct course of action. Then, when the Big Man believes that consensus is close at hand and that further talk will add nothing of value, he incisively summarizes the main arguments, indicates which have been rejected, and finally announces the decision reached by the clan. (pp. 77-8)

Sometimes . . . real consensus is impossible to achieve. For instance, although most of the assembly, including the Big Men, agree that . . . war is the only feasible choice, significant minority may hold out against this view. When it is clear that no amount of exhortation will change their opinion, the Big Man announces that the pro-war majority will proceed with preparations for an attack; but he warns them that, having overruled the opposition, they must be ready to pay most of the costs – in particular, compensation for allied and enemy deaths will fall mainly on them. At the same time he reminds the cautious minority that those who do not fight in support of the clan's interests cannot expect to enjoy the fruits of victory – enemy land that the clan may seize or any homicide pigs coming to the clan. The dissidents acknowledge the force of the warning while emphasizing their own prerogative of contributing few or no pigs to the homicide compensation.

To understand this consensually oriented decision making process and the relation of words to deeds, it is important to examine not only the debate but the practical behavior that follows:

. . . even as both parties are making clear their positions, everyone knows that, because the clan's survival may be at stake, once combat begins the doves will almost certainly be in their accustomed places fighting strenuously alongside the hawks. Moreover, many of them will probably join in the payments of homicide compensation, not merely to establish claims to whatever wealth the clan may secure but also, and equally important, to maintain their own reputations and that of the group. (Meggitt 1977, p. 79)

This account describes several egalitarian social conventions. The leader is not an autonomous thinker who imposes his decision on the group but rather part of a feedback process that involves all members of the group and takes hours to produce a decision. Decision making at any level requires a weighing of alternatives, which is inhibited by social pressures to conform. These pressures are relaxed during the decision-making process but strongly imposed afterwards, creating a behaviorally uniform group that acts as a unit. It is hard for natural selection to act within groups when there is no behavioral variation within groups for it to act on (Boyd & Richerson 1985; 1990b)! When groups cannot reach a consensus, creating important behavioral variation within groups, the costs and benefits associated with the alternative behaviors are carefully regulated. Doves cannot exploit Hawks by sharing the spoils of war, and Hawks cannot exploit Doves by expecting them to share the costs. Finally, nepotism within the group is conspicuously absent, although the entire group may be a kinship unit relative to other groups.

We agree that humans are often nepotistic in tribal societies but in some contexts they seem to avoid nepotism in favor of egalitarian social organizations and even scorn nepotism in a manner that resembles the Hutterites. The specific contexts in which nepotism is exchanged for egalitarianism call for study but seem to involve enterprises that require relatively large groups of people to perform successfully – warfare, collective labor, and hunting for large game where the probability of individual success is low. To these we might add the more nebulous but equally important contexts of decision making and memory for culturally transmitted information, which may be more successfully accomplished by relatively large groups. All of these contexts existed throughout the human past, perhaps favoring an evolved capacity to construct and live within egalitarian social organizations.

The fact that human groups usually fission along kinship lines is not an argument against group selection and even improves the conditions for group selection by increasing genetic variation among groups. Human groups (including religious groups) often fission in response to a conflict of interest within the group. In this case the fissioning event is not part of the egalitarian social organization, as it is with the Hutterites, but reflects the failure of the social organization to be egalitarian. Similarly, the fact that fitness correlates with status in many societies is not, by itself, an argument against group selection. As Miller notes, some forms of reproductive competition within groups can actually be favored by group selection. These broad patterns, which are presented as evidence against group selection, are being described at too coarse a scale. We must evaluate the fitness consequences of traits within and between groups with greater precision before we can decide how they evolved (Simpson). Finally, we are not trying to interpret *all* aspects of human behavior as products of group selection. Some of the evidence against group selection, such as the existence of fitness differences within groups, may well turn out to be evidence against group selection when it is examined in more detail. Our suggestion is that the Hutterites are an extreme example of an evolved *facultative* capacity, which means that comparable social orga-

nizations will be found only in some human groups and for some contexts but not others. We think group selection has been a strong force but not the only force in human evolution. We tried to make this point clearly in our target article but evidently we must make it again and again.

R2.3. Culture and group selection. We did not do justice to cultural influences on human behavior in our target article and welcome the opportunity to treat them briefly here. (See also **Brace, Campbell & Gatewood, Griffiths & Gray, Rapoport, Smith.**) Cultural explanations are often treated as an alternative to evolutionary explanations (Tooby & Cosmides 1992). The evolved mind is supposed to set very broad limits on human behavior (e.g., hunger and sex drives) but culture rather than evolution explains how humans behave within these limits. **Batson** uses this reasoning and his comments are therefore directed against human evolutionary psychology in general rather than group selection theory in particular.

Two more recent views of culture and evolution have emerged over the past two decades. In the first, culture is modeled explicitly as an evolutionary process in which alternative cultural units (variously called "memes," "culturgens," and so on) replace each other by differential transmission. The process of cultural transmission is influenced by the innate structure of the mind, which creates a complex relationship between genetic and cultural evolution. Cultural evolution acts partially in the service of biological fitness, or else the genes that shape cultural evolution would not have been selected over their alternatives. On the other hand, cultural evolution has its own transmission rules and is not expected to favor the same behaviors as genetic evolution in each and every case. Even within genetic evolution, a variety of transmission rules exist that select for different traits (e.g., maternal vs. bi-parental inheritance). We can expect an even greater diversity of outcomes when cultural traits are inherited not only from parents but also from peers, teachers, and so on (**Brace, Rapoport**; also see **Boyd & Richerson 1985; Findlay 1992**).

When cultural evolution takes place in a metapopulation, the level at which the cultural units are selected can be analyzed in the same fashion as genetic units. Thus, invoking culture does not make group selection go away but merely changes the details. For example, Boyd and Richerson (1985; 1990a) model conformity as the cultural transmission rule, "imitate the majority behavior in your group." This rule eliminates behavioral differences within groups and therefore concentrates cultural evolution at the among-group level. Some authors have concluded from this and other models that cultural group selection is more powerful than genetic group selection, perhaps accounting for the high degree of prosocial behaviors in humans (e.g., Campbell 1994; see also **Dugatkin, Rapoport, Smith**). We consider this conclusion premature because it depends on the details of the transmission rules. Even the conformity rule makes it difficult to understand the origin of variation among groups, because mutant cultural traits must somehow become frequent enough within a group to be imitated by others and persist. (A possible solution to this problem is offered

below.) As another example, the transmission rule "imitate the most successful person in your group" will favor behaviors that maximize cultural fitness relative to others within the same group and will be totally insensitive to group-level consequences. Even when cultural traits do spread via the survival and reproduction of whole groups, their rate of evolution can be very slow (Soltis et al. 1992). Natural selection in metapopulations is a complex process for both cultural and genetic traits, making simple generalizations elusive.

According to the second, more recent view of culture and evolution, "culture" has been overextended as an explanation of human behavioral variation. As a provocative example, Tooby and Cosmides (1992) ask us to consider a population of sophisticated juke boxes that are distributed over the globe. All juke boxes are identical, have thousands of songs stored in their memory, and are equipped with a clock and sensors that measure longitude and latitude to the nearest degree. The juke boxes are programmed to use the date and position on the globe as environmental inputs that determine which song is played. The juke boxes therefore play the same songs within locations, different songs between locations, and the songs at each location change over time. If the juke boxes were humans and the songs were behaviors, we would regard these differences as "cultural," yet there is no cultural transmission or even individual learning in this example. Tooby and Cosmides and other contributors to Barkow, Cosmides and Tooby (1992) portray the human mind as a sophisticated juke box with many "Darwinian algorithms" that evolved to solve important adaptive problems in ancestral environments and are triggered by appropriate environmental stimuli.

Although the juke box metaphor is obviously a caricature of human psychology (as Tooby and Cosmides acknowledge), it does reveal that our vocabulary for describing differences between cultures is impoverished. Few people would classify innate context-dependent behavior as cultural, yet, as our previous sentence attests, it is hard to avoid using the word "culture" when discussing human groups that behave differently from each other. Tooby and Cosmides (1992) propose a more complex vocabulary that should be considered when discussing examples such as the Hutterites.

These two views of culture and evolution are not yet well integrated with each other. Cultural evolutionary models are derived from population genetics models in which the transmission rules are very simple. This may be a good starting point but real transmission rules are probably like Darwinian algorithms in their complexity and adaptive design that guides cultural evolution to biologically adaptive outcomes. Tooby and Cosmides usually treat the environment as a mere button-pusher and have not yet integrated open-ended processes of individual learning and cultural evolution into their view of evolutionary psychology. We think that when the middle ground is explored, at least some complex transmission rules will be highly favorable for cultural group selection. For example, Boehm's (1994) account of the Mae Enga quoted above shows that groups can be behaviorally uniform, as in Boyd and Richerson's conformity model, and also have the capacity to change their behavior as the result of a rational decision-making process.

R2.4. Group selection and the adaptationist program. It is suggested by Wills that the study of group-level adaptations in humans will be exceptionally difficult. We agree in part, but we also wish to emphasize some of the simpler insights that can be achieved by group selection theory.

It should not be forgotten that our target article is basically a view of how to pursue the adaptationist program, which is remarkable for its simplicity and not its complexity. When we ask questions about the adaptedness of traits, we must recognize that functional design can exist at more than one level of the biological hierarchy. In addition to asking, "What would individual organisms be like if they were well adapted?" we must ask, "What would groups be like if they were well adapted?" These two questions bracket the possibilities and the actual outcome of natural selection will lie somewhere in between. The alternative procedure, of denying the existence of group-level adaptations even as we peer at them through the distorted lens of individualism, is not acceptable.

Complexities arise when we pursue any particular adaptationist hypothesis, but there is no reason to assume that these are insurmountable. We think the best way to begin is by ignoring proximate mechanisms and focusing on fitness differences at the phenotypic level (Goodnight). For any trait that is expressed by humans or other species, our procedure makes it relatively simple to determine the fitness consequences of that trait, relative to other traits, at various levels of the biological hierarchy. For example, it is easy to show that female-biased sex ratios are selected against within groups and favored at the group level. The only alternative procedure is to average the fitness of lower-level units across higher-level units to reach the bottom-line conclusion concerning what evolves. We hope we have convinced the reader that these two procedures are different ways of processing the same information and cannot be used to argue against each other. In particular, using the averaging approach does not constitute evidence against group-level adaptations. If we are interested solely in the bottom-line conclusion of what evolves, the averaging approach may be computationally simpler. However, if we are interested in determining the level(s) of functional organization, there is no alternative to monitoring natural selection separately at each level of the hierarchy before calculating the bottom-line conclusion of what evolves.

Knowing the fitness consequences of traits at the phenotypic level tells us what would evolve by natural selection if the environment were held constant and the traits had a simple genetic basis. Of course, most human behaviors do not have a simple genetic basis. There is no gene for pulling our hand away from the fire, but we still express the behavior under appropriate circumstances and it is biologically adaptive to do so. Natural selection has obviously endowed us with proximate psychological mechanisms that, to some extent, cause us to do the right things at the right times. Theories in traditional psychology (e.g., operant conditioning) require this assumption as much as theories in evolutionary psychology (e.g., cheater detection modules); the only difference is the assumed sophistication of the psychological mechanisms (Symons 1992; Tooby & Cosmides 1992). The next stage in the analysis therefore is to investigate the nature of these

proximate psychological mechanisms. The question is: "How must we modify this investigation to accommodate group selection?" The answer is: "Not much." Our proximate mechanisms should be sensitive only to the evolutionary success of behaviors and not to the level(s) at which they succeed. The social convention of drawing straws succeeds at the group level, but our proximate psychological mechanisms make it seem as reasonable to us as pulling our hand away from the fire. Abandoning one's personal identity for a group identity may feel great and appear reasonable in some situations, but the advantages of behaving that way exist at the group level. More generally, if a given behavior would evolve by group selection, our proximate mechanisms should cause us to express that behavior under appropriate conditions, just as if it had evolved by within-group selection. This returns us to the point we made earlier, that a theory of proximate psychological mechanisms does not map directly onto a theory of natural selection as a hierarchical process. The fact that we feel like doing something emotionally or decide to do something cognitively means at most that it was, on balance, evolutionarily successful in ancestral environments. The level at which it succeeded can be determined only by examining fitness effects.

To summarize, group selection theory does not make the adaptationist program insurmountably difficult. The main modification is to monitor natural selection separately at each level of the biological hierarchy before calculating the bottom-line conclusion of what evolves. In any case, there is no alternative if we want to determine level(s) of functional organization in humans and other species.

R2.5. Evaluating group selection. As we stated in our target article, the group selection controversy would make a fascinating case study for historians of science (see also Burghardt, Dupré). Moore cites the prominence of the "holdouts" as evidence that group selection has not yet "won over biology." We never claimed otherwise and what we did say is accurate: "a large group of knowledgeable biologists who are perfectly comfortable with the hierarchical approach . . . coexists with another large group whose members adhere to the earlier view" (sect. 1.6, para. 13). Both groups contain prominent biologists, so reputation and expertise do not explain the persistence of the controversy. It is important to remember that the group selection controversy in biology is a manifestation of a more general conflict between group and individualistic perspectives that exists throughout the human sciences and in everyday thought. Biologists are closer to a resolution than anyone else, and it is possible that group selection theory itself will explain why group- and individual-level perspectives tend to coexist in human thought. In any case, appeals to reputation are no substitute for a direct evaluation of the theory (Burghardt). History has shown that great scientists with well-deserved reputations are sometimes wrong and sometimes *never* change their minds. We hope that readers will not wait for the major gene-centered theorists to give their assent before evaluating group selection theory for themselves.

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Letters **a** and **r** appearing before authors' initials refer to target article and response respectively.

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