

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. "Naïve" 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.

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?

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-