The Poverty of Pluralism: A Reply to Sterelny and Kitcher

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The Journal of Philosophy, Vol. 87, No. 3. (Mar., 1990), pp. 151-158.

Stable URL:
http://links.jstor.org/sici?sici=0022-362X%28199003%2987%3A3%3C151%3ATPOPAR%3E2.0.CO%3B2-K

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COMMENTS AND CRITICISM

THE POVERTY OF PLURALISM: A REPLY TO STERELNY AND KITCHER

In *The Nature of Selection,*[1] I argued that "genic selectionism" is an ambiguous thesis. The view of natural selection that this label denotes was developed by George Williams in his landmark book *Adaptation and Natural Selection.*[2] It then was popularized by Richard Dawkins in *The Selfish Gene;*[3] later, Dawkins elaborated and somewhat reformulated the idea in *The Extended Phenotype.*[4]

In saying that genic selectionism is ambiguous, I meant that the thesis has a trivial and a substantive formulation. I claimed that Williams and Dawkins confused these; they repeatedly conclude that the substantive thesis is true when all their arguments demonstrate is that the trivial version is correct.

The substantive thesis might roughly be expressed by saying that all adaptations exist solely because they benefit individual genes (or genotypes). The trivial thesis is the idea that all natural selection can be "represented" in terms of genes and their properties. Both these formulations require clarification, which I tried to provide in my book.

In a recent article, Kim Sterelny and Philip Kitcher[5] defend a version of genic selectionism and attempt to refute the criticisms I made of that doctrine. Their defense has two components. First, they find fault with the account I gave of the units-of-selection controversy—an account which uses the idea of probabilistic causality as a tool of explication. Second, they provide a positive account of their own of what that controversy concerns, one which they think allows genic selectionism to emerge as a successful thesis.[6]

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[1] Cambridge: MIT, 1984. Hereafter NS.

[2] Princeton: University Press, 1966.

[3] New York: Oxford, 1976.

[4] San Francisco: Freeman, 1982.

[5] "The Return of the Gene," this JOURNAL, LXXXV, 7 (July 1988): 339–361. Cf. also Kitcher, Sterelny, and Waters, "The Illusory Riches of Sober's Monism," this JOURNAL, this issue, 158–161.

[6] The principal claims advanced by Sterelny and Kitcher are also developed by Ken Waters, "Environments, Pragmatics, and Genic Selection" (address to the American Philosophical Association, Eastern Division, 1985) and *Models of Natural Selection: From Darwin to Dawkins* (doctoral dissertation, Indiana University, 1986); see also his "Tempered Realism about the Forces of Selection" (forthcoming). John Cassidy defends a conventionalist thesis about the units-of-selection controversy in "Philosophical Aspects of the Group Selection Controversy," *Philosophy of Science,* XLV (1978): 575–594.

0022-362X/90/8703/151-8

I believe that the position they sketch is mistaken, both in its general orientation and in its details. I believe that the Sterelny/Kitcher position misunderstands what the biological question of the units of selection is about and that their criticisms of my own proposal are mistaken as well. Due to limitations of space, I shall focus on the positive proposal that Sterelny and Kitcher advance.

The idea of genic selectionism arose as an answer to a question. The question was an old one, predating (though surviving into) the modern synthesis' integration of Mendelian genetics and the theory of natural selection. The general question would now be formulated by asking what the "units of selection" are. But the pressing special case of this question—the one that drove the problem from the time of Darwin and Wallace at least until Williams's 1966 book—was whether adaptations evolve in nature because they are good for the group (or species) in which they occur. Williams's book delivered an emphatic *no* to this question about group adaptation. Group adaptations require the process of group selection.[7] Williams argued that virtually no solid evidence exists for group selection and that it is more parsimonious to hold that group adaptation is rare, if not nonexistent.[8] But rather than return to the traditional idea that adaptations exist for the good of the organisms possessing them, Williams opposed the idea of group adaptation by invoking a new alternative. This was the idea that the gene—not the group or the individual organism—is the unit of selection. Genic selectionism was born as an alternative to the idea of group selection.

To defend this new thesis, one must do more than reject the ideas of group selection and group adaptation. It was at this point that the fundamental ambiguity in the genic-selectionist position emerged. Williams and Dawkins placed heavy emphasis on the idea that all natural selection processes can be "represented" in terms of the fitness values of individual alleles (or genotypes).[9] Somehow this fact was supposed to support a substantive thesis. What they did not

[7] Roughly speaking, an adaptation is a trait that exists because there was a selection process of a certain sort. A trait is a group adaptation, as opposed to simply providing a fortuitous group benefit, only if it evolved because it conferred a group benefit.

[8] Although Sterelny and Kitcher say that discussion of parsimony in connection with the units-of-selection issue is "unnecessary dust" kicked up by philosophers (340), I believe that credit should be given where credit is due. Parsimony and a variety of other philosophically loaded concepts are repeatedly pressed into service by Williams and Dawkins. Such considerations were not invented by card-carrying philosophers, but were put into play by the scientists themselves.

[9] An explication of what it means to "represent" a selection process in the vocabulary of genes and gene frequencies, and an explanation of why this fact about representability cuts no ice in the units-of-selection controversy, is provided in NS, ch. 7.

realize is that the point about representation is a truism; it would be correct even if group selection and group adaptation were ubiquitous.

It is an empirical question whether there are group adaptations. Properly formulated questions about group selection require detailed information about population structure to be answered. More generally, I would claim that substantive biological questions about the units of selection have always been empirical. Hence, a litmus test for any philosophical clarification of this scientific problem is that it clearly identify what the empirical issues really are.

Sterelny and Kitcher advocate a pluralistic view of this controversy. According to them, there are always "alternative, maximally adequate representations of the causal structure of the selection process" (358). I believe that there is a sense in which they are right—but it is trivial and utterly disconnected from the biological problem. To illustrate what I have in mind here, I shall describe a case of group selection and group adaptation. Then I shall describe what Sterelny and Kitcher's pluralism would say about the case in question.

Just as the focal point of the units-of-selection controversy has been the issue of group selection, so the focal point of the group-selection controversy has been the issue of altruism. An altruistic characteristic[10] of an organism is one that hurts the individual that has it while helping the group within which the individual lives. Help and hurt are calculated in the currency of survival and reproductive success—of fitness. The opposite trait—"selfishness"—leads its bearer to enjoy the donations provided by altruists, even though selfish individuals do not reciprocate. Selfish individuals are free riders. In a single population made of altruists and selfish individuals, altruists will be less fit than selfish individuals, and so (with the usual assumptions about heritability, etc.) the population will evolve to a state in which altruism has disappeared.

The following graph of the fitnesses of altruists (A) and selfish individuals (S) illustrates two fundamental facts about these characteristics. No matter what the mix is within a group of As and Ss, the A individuals are on average less fit than the S individuals. The fitness of a group however (as measured by the average fitness of the organisms in it, $\bar{w}$), is enhanced by containing high concentrations of altruists.

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[10] In the evolutionary, not the psychological, sense of that term. I discuss the difference in "What is Evolutionary Altruism?", B. Linsky and M. Matthen, eds., *New Essays on Philosophy and Biology* (*Canadian Journal of Philosophy* Supplementary Volume), XIV (1988): 75–99; and in "What is Psychological Egoism?" *Behaviorism* (forthcoming).

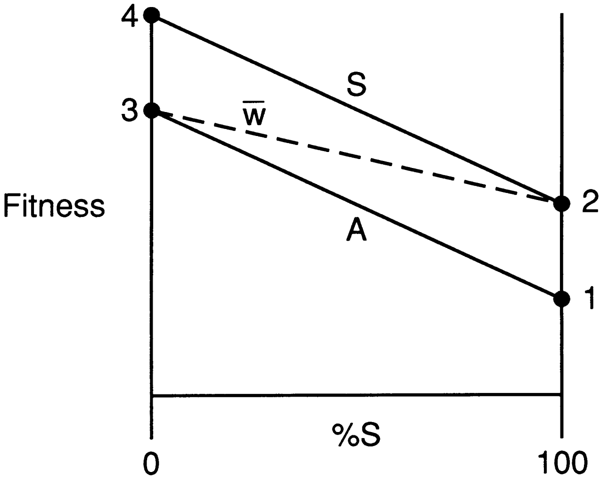

Figure 1

I said before that, if the two traits evolve in the context of a single cohesive population, *S* will displace *A*. This need not be true, however, if a process of group selection is underway. Imagine that we have an ensemble of groups, each containing some mix of *A* and *S*. If certain contingent conditions are satisfied, *A* can evolve and be maintained in the ensemble.

The following two biological conditions roughly suffice. First, let like live with like. Second, let the populations fragment and found new colonies fast enough (i.e., before the process of individual selection at work within each group drives *S* to fixation). Even though I have stated these biological requirements in only a rough and qualitative way, the main conceptual difficulty in understanding how altruism can evolve under group selection may now be stated: If *S* is fitter than *A* within each group (a definitional truth), how can *A* evolve? Within each group, *S* is declining in frequency. Does this not mean that *S* must disappear from the ensemble of groups?

A beginning of an answer comes from the requirement that like live with like. Imagine that the ensemble consists of 200 organisms, which live in two groups of 100 individuals each. The first group is 99% *S* and the second is 1% *S*.[11] Below are the average fitnesses (the *w*s) of selfish and altruistic individuals within each group, and the overall average fitnesses of the two traits. I have used the numbers on

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[11] Note that the global frequencies of *A* and *S* are each 0.5; yet, most altruists live in a group in which the frequency of altruism is far greater than 50%. This is part of what I mean by 'like living with like'; there is no requirement that the groups be internally homogeneous.

the y-axis in the above figure to represent fitnesses (think of them as expected numbers of offspring if you like, or as arbitrary fitness units):

Group 1	Group 2	Overall Average
(99) $w_{S1} = 2$	(1) $w_{S2} = 4$	(100) $w_{S.} \approx 2$
(1) $w_{A1} = 1$	(99) $w_{A2} = 3$	(100) $w_{A.} \approx 3$

This is an example of Simpson's paradox;[12] inequalities true within each group reverse when one averages over all groups. Within each group, selfish individuals are on average fitter than altruists, but (in this example), the reverse is true when one considers the two population ensemble as a whole.[13]

For altruism to increase in frequency under group selection, altruists must be fitter than selfish individuals in the global ensemble. The fact that altruists are less fit within each group does not rule out that possibility. Rather, if like live with like, Simpson's paradox can take hold, and the altruistic trait can increase in frequency.

If the kind of process just sketched led a genuinely altruistic characteristic to evolve, a biologist would rightly see group selection at work. On the other hand, if selection occurs exclusively within the confines of a single cohesive population, then biologists would be right to view group selection as a fantasy. And if natural populations sometimes are one way and sometimes the other, then different answers about the units of selection would be appropriate in different cases. It all depends on the biology.

This may sound like pluralism, but it is not the pluralism that Sterelny and Kitcher espouse. I claim that, if an altruistic character evolves in the kind of circumstances just described, then one must interpret this as a case of group selection; Kitcher and Sterelny claim that all selection processes, including this one, can be described in a number of equally correct ways. Even if the process I have just described occurred in nature, they would say that there are many correct descriptions of it, ones which generate different answers to the question of what the units of selection are.

To show what this means, I shall add a further detail to the example. Let *A* and *S* be traits in a plant species in which an individual may manufacture an insecticide at some energetic cost to itself and then

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[12] For philosophical discussion of the meaning of Simpson's paradox and its importance for understanding causality, see Nancy Cartwright, "Causal Laws and Effective Strategies," *Nous,* XIII (1979): 419–437.

[13] This example does not illustrate how *A* can increase in frequency after it is introduced by a single mutant or migrant. Rather, the point is to show how *A* can increase in frequency even though there is individual selection against it within each group.

leach the chemical into the soil. Imagine that the insecticide protects not just the plant that produces it, but the plants that live near the producer as well.[14] If so, producing the insecticide and leaching it into the soil would be an altruistic trait. The selfish alternative would be the trait of not producing the insecticide. I am supposing that *S* individuals receive the benefit of the insecticide without incurring the energetic cost of producing it.

So *S* and *A* are phenotypic characteristics. What about the genetics? Suppose the organisms in question are haploid and that the two phenotypes are controlled by a single gene. Individuals with the *a* allele (at a given locus) produce the insecticide; individuals with the *s* allele do not. Under group selection, the *A* phenotype evolves; and so, of course, does the *a* gene.

Kitcher and Sterelny think that the following three statements are true of the process I have described:

(i) Groups that contain high frequencies of altruists do better than groups that do not; the reason is that containing lots of altruists is good for the group.
(ii) Altruistic individuals on average do better than selfish individuals. The reason is that altruists tend to live together, so they usually do not get exploited by free riders.
(iii) The *a* gene on average does better than the *s* gene. The reason is that *a* genes tend to occur in groups in which there are mainly other *a* genes, so *a* genes usually do not get exploited by free-rider genes.

I agree that these are all true, but it seems to me that nothing interesting follows from that. If Kitcher and Sterelny's pluralism is simply the idea that there are different vocabularies (group, organismic, and genic) that can be used to describe what is going on here, then the thesis is trivial. What is biologically significant is the process, not how it is described. Genes cause organismic phenotypes, and the phenotypes of organisms determine the phenotypes of the groups in which they live. This much is undeniable. But it does not follow that the above process can be reinterpreted so that one no longer needs to think of it as involving group selection.

Here is another way to see why Sterelny and Kitcher's pluralism does not engage the biological issue. To address the units-of-selection controversy, one must say which objects in nature show significant degrees of functional organization and explain why this is so. Organisms typically show a very high degree of functional organization. Do groups? Arguments about what the units of selection are

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[14] For simplicity, suppose that a producer and the nonproducers that are its neighbors are protected to the same degree.

attempt to answer this question and explain why the answer is *yes* or *no*. I see no room for conventionalism here.[15]

Organisms can be viewed as groups of integrated genes. An organism is a group; individual genes are its parts. Just as the group-selection controversy shows that there can be conflict between what is good for the group and what is good for the individual organism, it also should be possible for there to be conflict between what is good for the organism and what is good for the individual gene.[16] In the group-selection case, it is a matter of contingent biological fact that group adaptations are rare; if the interests of organisms usually win out over the interests of single genes, that, too, will be a contingent biological fact, one that calls for explanation. Looked at in this way, the thesis of genic selectionism is substantive—as vulnerable to empirical test as the thesis of group selectionism. A formulation of it that turns it into a truism has deprived it of its biological interest.

Kitcher and Sterelny argue that there are certain sorts of selection processes that are not consistent with the idea that the individual organism is the unit of selection. Here they make a point that I had developed in my book—that meiotic drive involves selection at the genic, not the organismic, level. When it comes to altruism, they think that this, too, is a phenomenon that cannot be handled organismically. And, of course, it goes without saying that for them there are some characters that cannot be viewed as group adaptations. So, for them, the thesis that the organism is the unit of selection is vulnerable to empirical disconfirmation; it is true sometimes, but not always. And the idea that the group is the unit of selection has the same empirical status. Yet, curiously enough, their view is that the genic perspective can accomodate anything and everything that might happen in natural selection. I, on the other hand, think that the standards applied to test whether groups or organisms are units of selection also should be applied to genes. When this is done, a monolithic genic selectionism is no more empirically plausible than a monolithic thesis of organismic or of group selectionism.

Sterelny and Kitcher share my desire to distinguish trivial genic selectionism from its substantive alternative. They agree that it is trivial that "the result of selection is (almost always) an increase in

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[15] Unless one is prepared to be a conventionalist about causation, or about natural history, or about something far more global than the biological questions themselves. Sterelny and Kitcher do not seem inclined to take that radical route.

[16] For an interesting argument to the effect that fundamental facts about ontogeny are explained by the conflict of selection within organisms and selection between them, see Leo Buss, *The Evolution of Individuality* (Princeton: University Press, 1987). See also David Sloan Wilson and Elliott Sober, "Reviving the Superorganism," *Journal of Theoretical Biology*, CXXXVI (1989): 337–356.

frequency of some gene in the gene pool" (339). They claim that Dawkins advances a second thesis, however, one that is supposed to be biologically important to the units-of-selection problem; this is the idea that "barring complications, the average ability of the genes in the gene pool to leave copies of themselves increases with time" (340). My view is that this second thesis is more or less beside the point.

When group selection manages to increase the global frequency of the *a* gene, it will be true that the average fitness of genes in the global population increases. The average fitness of the alleles in the population (where these are perfectly correlated with their respective phenotypes) is depicted in the above figure by $\bar{w}$. On the other hand, when purely individual or genic selection within a single cohesive population eliminates both the *A* phenotype and the *a* allele, $\bar{w}$ will decline. Group selection can lead the average fitness of genes to increase and genic selection can lead the average fitness of genes to decline. How often this quantity goes up or down has little to do with what the units of selection are.[17]

In my book, I claimed that it often is useful to represent selection processes in a genic vocabulary. This technique has generated some confusions; it also has provided a number of important insights. But the utility of a mode of representation is not what the units-of-selection problem has been about. It is about the levels at which adaptations have accumulated. The pluralism of Sterelny and Kitcher confuses these two questions, in much the same way that Williams and Dawkins did earlier.

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THE ILLUSORY RICHES OF SOBER'S MONISM

Biologists have discovered that a wide variety of population-genetics models apply to cases of natural selection in the wild. The outcome of selection may depend on the number

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[17] Also, I am not aware that Dawkins has ever taken a stand on whether the average fitness of genes in a population typically increases. In *The Extended Phenotype* (p. 193), he mentions in passing that "many population geneticists are, for reasons best known to themselves, very interested in another quantity which is called the mean fitness of a population."

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