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# Realism, Conventionalism, and Causal Decomposition in Units of Selection: Reflections on Samir Okasha's *Evolution and the Levels of Selection*

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I discuss two subjects in Samir Okasha's excellent book, *Evolution and the Levels of Selection*. In consonance with Okasha's critique of the conventionalist view of the units of selection problem, I argue that conventionalists have not attended to what realists mean by group, individual, and genic selection. In connection with Okasha's discussion of the Price equation and contextual analysis, I discuss whether the existence of these two quantitative frameworks is a challenge to realism.

## Realism versus Conventionalism

The issue of realism versus conventionalism has been central to philosophical discussion of the units of selection problem. Realists maintain that it is a factual question whether an evolving trait is influenced by group, individual, and/or genic selection. Conventionalists (Sterelny and Kitcher 1988; Kitcher, Sterelny, and Waters 1990; Waters 1991; Sterelny and Griffiths 1999; Kitcher 2004; Waters 2005) deny this. For them, the relevant question concerns which type of explanation is most useful. True, you can sometimes say that a trait evolves because of group or individual selection, but you can also say that it evolves because of genic selection. The converse, however, does not hold; some cases of genic selection cannot be described as cases of individual or group selection. For conventionalists, the genic account has a pragmatic virtue—its greater generality. Conventionalism is not the position promoted by early foes of group selection (Williams 1966, Maynard Smith 1976, and Dawkins 1975) who argued that group selection hypotheses are factually mistaken claims about nature. According to conventionalists, the battle concerning group selection that started in the 1960s rested on a confusion. Biologists were mistaken in thinking that a substantive empirical issue was at stake.

I describe the alternative to realism as *conventionalism*, not *pluralism*, because realism about *units of selection* and pluralism about *explanation* are compatible. Or, at least, I hope they are, because I endorse them both. Explanatory pluralism is the view that, for any event, there are different true stories that each explain why the event occurred. Some describe more proximate causes while others describe causes that are more distal; some describe macro-causes while others describe causes that are more micro (Sober 1984, 1999). There is no objective sense in which one of these is best; some are more useful than others, depending on our interests. For example, consider the evolution of altruism and selfishness in groups of size two ($n = 2$ is chosen for convenience) where the fitnesses of the two traits are those shown in Table 1. If selection causes altruism to increase, the following explanations are both correct (Sober 1993):

(1) There is group selection favoring altruism and individual selection favoring selfishness, where the former cause is stronger than the latter.

(2) $\Pr(\text{partner is } A \mid \text{individual is } A) - \Pr(\text{partner is } A \mid \text{individual is } S) > c/b$.

This pluralism about explanation is perfectly compatible with realism in connection with units of selection. Setting aside some niceties for the moment, I define group selection as variation in fitness among groups, individual selection as fitness variation among organisms in the same group, and genic selection as fitness variation among genes in the same organism. I'll use the term "MLS theory" (multi-level selection theory) to label these definitions. According to MLS theory, a given trait may

Table 1:
The fitness of an individual depends on its own phenotype and on the phenotype of its partner.

| | | the individual's partner is | |
|---|---|---|---|
| | | Altruistic | Selfish |
| the individual is | Altruistic | $w + b - c$ | $w - c$ |
| | Selfish | $w + b$ | $w$ |

Table 2:
*M* is an evolving metapopulation that is divided into groups, which contain organisms, which contain genes. MLS theory and conventionalism assign different meanings to "individual selection" and "genic selection." They agree about what "group selection" means.

| | MLS theory | Conventionalism |
|---|---|---|
| Group selection | Variation in the fitnesses of groups in *M* | Variation in the fitnesses of groups in *M* |
| Individual selection | Variation in the fitnesses of organisms within groups | Variation in the fitnesses of organisms in *M* |
| Genic selection | Variation in the fitness of genes within organisms | Variation in the fitnesses of genes in *M* |

evolve because any mix of these processes is under way. The units of selection problem is as real as the question of how fitnesses vary.

Okasha (105–107)[1] debunks a conventionalist argument that has been in the background of this debate. Since group properties *supervene* on properties of individuals, it seems to follow that group properties can be explained in terms of properties of individuals. Okasha notes that "the supervenience argument, if correct, shows only that a character-fitness covariance at the higher level must be a byproduct of *some lower-level causal processes or other, not necessarily lower-level selection* [italics his]." I agree (Shapiro and Sober 2007), but conventionalists claim to have a reply. If the groups in the metapopulation vary in fitness because they have different frequencies of the two traits (*A* and *S*), and the frequencies of the traits change for that reason, then it must also be true that *A* and *S* individuals in the metapopulation have different average fitnesses. Conventionalists then define individual selection as variation in fitness among individuals in the metapopulation, and declare a victory. The concept of individual selection used here differs from the one used by MLS theory, according to which individual selection means variation in fitness *within groups*, not in the *global metapopulation*. A similar ambiguity attaches to the concept of "genic selection." When selection causes gene frequencies in the metapopulation to change, conventionalists define genic selection to mean variation in the fitnesses of genes in that global population. MLS theory restricts the term to variation in fitness that occurs within individual organisms; it occurs when there is meiotic drive or intragenomic conflict, but not universally. Table 2 provides a translation manual for MLS theory and conventionalism. The key difference is that the former takes group, individual, and genic selection to be logically independent, while the latter views them as linked by entailment relations.

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[1] All page numbers refer to Okasha (2006) unless otherwise noted.

Conventionalists about units of selection have suggested that their position resembles conventionalism about geometry (Sterelny and Kitcher 1988, 359); both involve claims about there being ‘‘no fact of the matter’’ as to which of several hypotheses is true. In fact, there is a difference. Geometric conventionalists and realists discuss the same alternatives—Euclidean and non-Euclidean geometries. But when MLS theorists discuss individual and genic selection, they mean something different from what conventionalists mean when they use the same words. Conventionalism and realism about geometry are incompatible philosophies, but conventionalism and realism about units of selection, apparently, are not, once the ambiguities are recognized. This polysemy is exasperating, but does it hold out the hope that we can all be friends? Well, I am happy to be a conventionalist about the descriptors that *conventionalists* use. What I don’t see is why conventionalists are entitled to take a conventionalist view of the distinctions that *realists* wish to draw.

Okasha (128–129) criticizes Kitcher’s (2004, 89) conventionalism, focusing on Kitcher’s statement that ‘‘one can tell all the facts about how genotype and phenotype frequencies change across the generations—including the causal explanations of the changes—without any commitment to a definite level at which selection acts.’’ Notice that Kitcher does not reject the factuality of causal talk in general; his scruples are more specific, in that he thinks that causal explanations can be given without invoking a uniquely correct ‘‘level.’’ Consider how Kitcher’s position applies to propositions (1) and (2). It is true that the evolution of altruism can be explained by citing proposition (2), which does not mention opposing forms of selection occurring at different levels. However, that does not address the question of why the claim made by proposition (1) is nonfactual. Nor does it address the more general question of why the distinctions drawn by MLS that are described in Table 2 are nonfactual. Sterelny and Griffiths (1999, 169) and Waters (2005) make the same mistake.

## Apportioning Causal Responsibility

Okasha wants a quantitative as well as a qualitative definition of group and individual selection. That is, he not only wants to get clear on what it takes for group and individual selection to occur; he also wants to describe how the total change in trait frequency produced by natural selection decomposes into the changes caused by selection at different levels. Indeed, Okasha regards the quantitative task as ‘‘more fundamental’’ (97). I’ll explain later why I don’t see the priorities in this way, but for now, let’s examine what Okasha says. He considers two proposals for effecting a quantitative decomposition—one based on the Price equation, the other on contextual analysis. Price's (1992) equation is specific to evolutionary theory; contextual analysis is a general statistical technique from multiple regression theory. Okasha does not object to the equation or to the technique *per se*, since he thinks that both produce valid *statistical* decompositions of total change into components. Rather, Okasha's question is whether they effect a proper *causal* decomposition of the selection process into its components. Table 3 describes the two decompositions. The Price approach cites $Cov(W,Z)$, the covariance of group phenotype ($Z$) and group fitness ($W$), and $E(Cov_k(w,z))$, which is the average covariance of individual phenotype ($z$) and individual fitness ($w$). The terms in the contextual decomposition will be explained shortly. Both approaches use the normalizing constant $\overline{w}$, which is the average fitness of the individuals in the metapopulation.

Okasha (99) presents three objections to the Price approach; I will concentrate on the first. It is related to a point I made in my 1984 book concerning a distinction that is central to understanding the difference between levels of selection (Williams 1966). We need to distinguish traits that evolve by group selection from traits that benefit the group though they evolve by purely individual selection. Okasha calls the latter *cross-level byproducts*; understanding this concept is a central project in his book. Consider two zebra herds; all the zebra in the first herd run fast and all those in the second run slow. Suppose that lions randomly select a zebra to attack, but that a zebra under attack has a better chance of escaping if it runs fast. Suppose further that a zebra's fitness is unaffected by what the other zebras in its herd are like. In this case, the intuitive conclusion is that there is purely individual selection. True, running fast is good for the herd, in that fast herds are less likely to be hunted to extinction than slow ones; however, the trait does not evolve *because* it is good for the herd. If the two herds are distinct groups, this example shows that group selection cannot be defined as fitness variation between groups. The Price approach gives the wrong answer here, since all the variance in fitness is between the two herds.

This problem can be solved by using an interactionist definition of group: a bunch of organisms is said to comprise a group (relative to a

Table 3:
The Price approach and the contextual approach propose different decompositions of the total change ($\Delta z$) in trait frequency due to natural selection into two components (93).

| | | Individual selection | | Group selection |
|---|---|---|---|---|
| Price approach | $\Delta z =$ | $E(Cov_k(w,z))/\overline{w}$ | + | $Cov(W,Z)/\overline{w}$ |
| Contextual approach | $\Delta z =$ | $\beta_1 Var(z)/\overline{w}$ | + | $\beta_2 Var(Z)/\overline{w}$ |

given trait *T*) precisely when their trait values for *T* affect each other's fitness. If lions prey on zebras in the way specified, the two herds don't count as distinct groups (with respect to running speed) and hence there is no group selection on that trait (Sober and Wilson 1994, 1998). The interactionist definition of group saves the Price approach from endorsing the counterintuitive judgment that running speed in this example evolves by group selection. Okasha (98) agrees, but says that a quantitative version of this problem persists even when the interactionist definition of group is used. His idea (pers. comm.) is that the Price approach can mistakenly interpret very weak group selection for very strong group selection. Suppose, to change the example, that fast zebras have fitnesses of $0.9 + n/10^{10}$ and slow zebras have fitnesses of $0.2 + n/10^{10}$, where $n$ is the number of fast zebras in the herd. If herds have a maximum size of 100, group context has a trivial effect on fitness; the overwhelmingly stronger influence is individual phenotype. Okasha thinks this means that only weak group selection is at work. However, because there is *some* sensitivity of an individual's fitness to group context, the two herds of zebra constitute groups in the interactionist sense of that term. If fast zebras live together and slow zebras do too (100%, or nearly so), the Price approach, when coupled with the interactionist concept of group, entails that all (or almost all) the selection is at the group level. Okasha thinks it is counterintuitive that there is no group selection in the first case while there is strong group selection in the second case depicted in Figure 1.

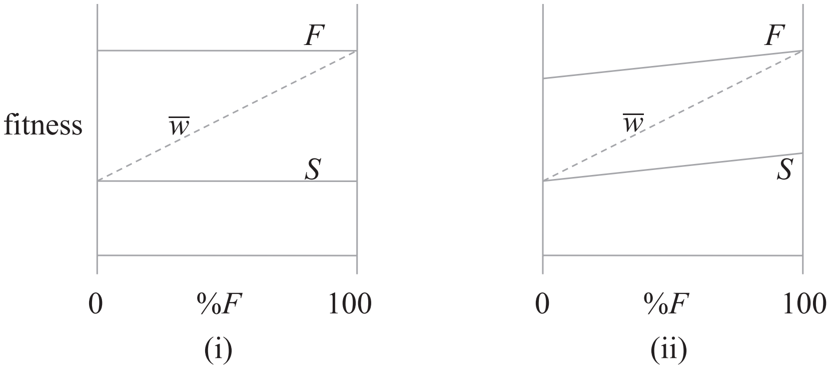

Figure 1: Two fitness functions for fast (*F*) and slow (*S*) zebra. The interactionist conception of groups, coupled with the Price approach, entails that (i) involves no group selection, since there are no groups, whereas (ii) can involve strong group selection. The average fitness of the individuals in a group is represented by $\bar{w}$.

The contextual approach provides what Okasha regards as the correct assessment of this example. It focuses on the question—*why* do individuals vary in fitness? If an organism's fitness depends strongly on its own phenotype and only slightly on the kind of group it occupies, the contextual approach concludes that there is strong individual selection and weak group selection. The contextual approach sees only a mild difference between (i) and (ii) in Figure 1; it says there is no group selection in the first case and very weak group selection in the second. It reaches this conclusion by defining individual- and group-selection as shown in Table 3. The coefficients $\beta_1$ and $\beta_2$ are terms in the standard regression model (87)

$$w = \beta_1 z + \beta_2 Z + e,$$

which means that an individual's fitness ($w$) is predictable from its own phenotype ($z$), the phenotype ($Z$) of the group it inhabits, and an error term $e$. According to this approach, the strength of group selection depends on the between-group variance in *phenotype*, not on how much groups vary in *fitness*.

This is why the contextual approach leads to counter-intuitive consequences when there is "soft selection" (95–96). Suppose groups vary in their frequencies of a trait and there is frequency dependent individual selection in each group on the trait, though all the groups have the same fitness (see Figure 2). The contextual approach concludes that there is group selection here because $\beta_2$ and Var($Z$) are both nonzero;

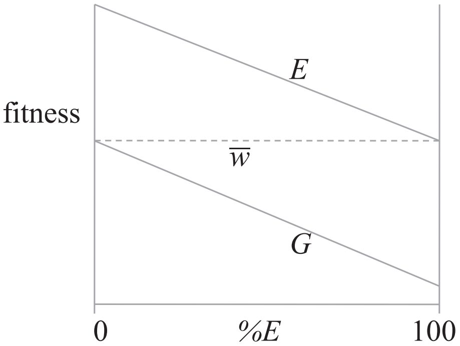

Figure 2: An example of soft selection. Although groups in the metapopulation differ in the proportion of *E* and *G* individuals they contain, each has the same expected productivity, represented by its value for $\bar{w}$. An individual's fitness depends on its own phenotype and on the kind of group it inhabits.

it doesn't matter that there is no variation in the *fitnesses* of groups. Okasha regards this as a counter-intuitive conclusion, as do I. Group selection should "push" the metapopulation in the direction of traits that are good for the group; individual selection should do the same with respect to traits that are good for the individual. In Figure 2, individual selection favors trait *E*, but what does group selection favor? The answer is: *nothing*.

Although Okasha recognizes the limitations of both the Price and contextual approaches, he says that, on balance, he favors the latter (99). His views concerning the successes and failures of the two approaches lead him to a nihilistic conclusion (157): "there cannot be a fully general solution to the problem of causally decomposing the total evolutionary change..." This conclusion goes beyond his evaluation of the two approaches. Even if he were right about them, it wouldn't follow that there is no third approach that is better.

## A Point of Consensus

Although the Price approach and the contextual approach disagree about fast and slow zebras, and also about soft selection, there is something on which they agree. This is the case of altruism and selfishness evolving in a metapopulation in which groups vary in fitness. The relevant fitnesses are shown in Figure 3. Each criterion says that the expected change in frequency of altruism is the sum of a negative term (representing individual selection against altruism) and a positive term (representing group selection favoring altruism). The sums computed by the two approaches must be equal, which means that *the two approaches agree on whether individual selection is stronger than group selection*. However, they may disagree about the numbers. For example,

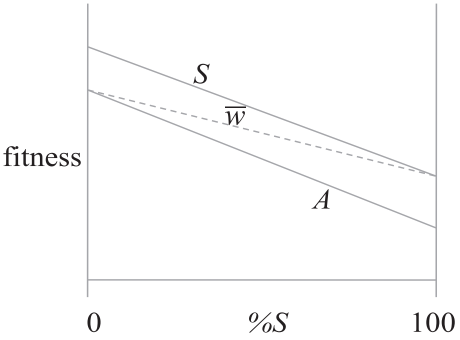

Figure 3: The evolution of altruism (*A*) and selfishness (*S*). Group selection favors the former, individual selection the latter.

one approach might say that altruism will increase by 7% because group selection predicts a 10% increase and individual selection predicts a 3% decline, while the other says that the 7% increase will occur because group selection predicts a 15% increase while individual selection predicts an 8% decline.

## Three Grades of Realism and Conventionalism

The contrast between realism and conventionalism is too simple. We need to distinguish three questions about a trait in a metapopulation that experiences natural selection:

> (Quant) How much of the total change due to natural selection is due to individual selection and how much is due to group selection?
>
> (Comp) Which has the stronger effect on the total change due to natural selection, individual selection or group selection?
>
> (Qual) Is individual selection occurring? Is group?

There is a realist and a conventionalist position on each question. Realism about questions higher on the list entails realism about items lower down, but not conversely. And conventionalism about items lower on the list entails conventionalism about items higher up, but not conversely. Qualitative realism is therefore consistent with quantitative conventionalism. Of the three realisms, the qualitative form is most fundamental, since it is presupposed by the others. Conventionalists have boldly espoused a conventionalism of the strongest sort, in that they have denied that qualitative questions about units of selection have factual answers. Realists have been more cautious; they have defended a modest variety of realism, since they too have addressed the qualitative question.

When groups are defined by fitness interactions, the Price and contextual approaches almost always agree about the qualitative facts. Soft selection is an exception. Even if qualitative conventionalism made sense for soft selection, that would not justify qualitative conventionalism across the board. Since the two approaches rarely assign the same numerical values to the magnitude of group selection, this may seem to motivate quantitative conventionalism, though, as mentioned, maybe there is a third and better approach. If disagreement supports conventionalism, then agreement supports realism, in which case the agreement of the two approaches about whether individual or group selection is stronger when altruism evolves supports a comparative realism.[2]

Even if we are qualitative realists, quantitative realism requires further argument. When group and individual selection both affect the evolution of a trait, is there a uniquely correct answer to the question of how strong each cause is? It is pointless to speculate about this in the abstract. We need to get down to details concerning how a causal partition might be effected. It is one of the many merits of Okasha's book that he does so.

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[2] Does this trifurcation of questions about realism and conventionalism arises in other scientific problems? It does in *philosophy*. Bayesians agree on what it means for an observation to confirm a hypothesis, but there are numerous Bayesian proposals concerning how degree of confirmation should be measured (Fitelson 1999). Even if there is a fact of the matter as to whether $O$ confirms $H$, this does not entail that it is a matter of fact how much $O$ confirms $H$.

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