

TESTING ADAPTATIONISM: A COMMENT ON ORZACK AND SOBER

One of the most heated areas of controversy within contemporary evolutionary biology concerns adaptationism and the importance of natural selection relative to other evolutionary factors. Because these debates sometimes seem to be more ideological than scientific, Orzack and Sober's (1994) recent suggestion about how to test adaptationism is likely to be well received. However, as we will show, both their statement of the hypothesis of adaptationism and their method of testing it are seriously flawed. We will try to refine the relevant hypotheses and consider the extent to which, and the methods by which, they can be tested. In this way we do take Orzack and Sober's project seriously. But, we wish to state at the outset that the status of the "adaptationist program" does not stand or fall on the outcome of their project or our revision of it here. That is, even if the hypothesis of adaptationism cannot be stated in a precise enough manner to be testable, or if it is so stutable but proves to be false, the value of an adaptational approach to evolutionary biology is not necessarily diminished (see Mayr 1983 and Williams 1992 for further discussion). Nonetheless, we think it uncontroversial that in science a well-posed thesis is preferable, everything else being equal, to an ill-posed or untestable one, and our purpose here is to demonstrate that Orzack and Sober's thesis of what constitutes adaptationism is ill posed.

ORZACK AND SOBER'S STATEMENT OF ADAPTATIONISM

The claim that adaptationism is a testable hypothesis is one that many evolutionary biologists would find far from obvious. Some would think of adaptationism as a research strategy (e.g., Mayr 1983); others would think that as a hypothesis it is simply too vague to be tested (e.g., Lewontin 1978; Gould and Lewontin 1979). Orzack and Sober recognize this ambiguity and set out to clarify the definition of adaptationism. They begin by distinguishing three statements concerning a trait T of an individual in a population (Orzack and Sober 1994, p. 362):

- (U) Natural selection played some role in the evolution of T . (U stands for ubiquitous since we believe this proposition applies to most traits.)
- (I) Natural selection was an important cause of the evolution of T . (I stands for important.)
- (O) Natural selection is a sufficient explanation of the evolution of T , and T is locally optimal. (O stands for optimal.)

According to Orzack and Sober, "These propositions are presented in order of increasing strength. Proposition (O) entails (I) but not conversely, and (I) entails (U) but not conversely" (p. 362). In this discussion, we will focus on (O), as Orzack and Sober did, and on its generalization, which we label (A) for adaptationism:

- (A) Natural selection is a sufficient explanation for most nonmolecular traits, and these traits are locally optimal (Orzack and Sober 1994, p. 364).

Orzack and Sober take (A) to be a reasonable generalization of (O) since they think that adaptationism should not be saddled with the stronger universal claim that all traits are sufficiently explained by natural selection and that all traits are locally optimal. We agree with this.

AMBIGUITY IN (O)

In this section we will show that there are two important ambiguities in their statement of (O). The first concerns the notion of sufficient explanation. The second concerns the intended backward time scale of these explanations. These ambiguities prevent a clear interpretation of whether evolutionary change is consistent with the adaptationist view.

What do Orzack and Sober mean by sufficient explanation? They "define the concept of sufficient explanation by reference to the predictions one obtains from a 'censored' model (i.e., a model in which the only evolutionary force is natural selection)" (p. 363). In particular, a model involving only natural selection is deemed a sufficient explanation if (1) the model predicts a final state *T* in a population and observations are, within the limits of estimation error, consistent with this prediction and (2) all individuals in the population exhibit the same phenotype or distribution of phenotypes.

The difficulty with criterion 1 is that failing to reject the selection (O-type) model says nothing about whether there are other, I-type or U-type models that might also fail to be rejected when their predictions are compared with observations. This is particularly likely to be a problem when O-type and I-type models predict the same evolutionary endpoint but differ in the trajectory by which that endpoint is reached. Since both models predict the same final state, they both satisfy criterion 1. Criterion 1 thus a priori gives precedence to an O-type model over equally explanatory I-type models if an O-type model can be shown to be consistent with the data. This precedence is problematical, however, if making the statement that something is an adaptation is taken to imply something about the actual processes that moved a population to state *T*, an implication with which we believe most evolutionary biologists would agree (but see Williams 1992, sec. 4.1, for an exception). In that case, the extreme assertion of adaptationism, analogous to Orzack's and Sober's proposition (O), is that natural selection was the only important force involved in the evolution of the population to state *T*.

The only way this type of statement can be reasonably accepted is to demonstrate not only that an O-type model is consistent with final state *T* but also that

no plausible I-type (or U-type) models are also consistent with state *T*. A detective who finds a body in a house that has just burned down does not automatically conclude that the fire was the cause of death, even though the fire model predicts death; that is, fire can cause death and the person is dead. Because there are other possible and plausible causes of the person's death, the detective should resist this inference. Put conversely, only after eliminating other plausible possibilities should the detective conclude that fire was the cause of death. Likewise, since *T* can be fixed in a population by other means, evolutionists should be wary of inferring (O) from the observation of fixation of *T*. In other words, Orzack and Sober's criterion 1 is incomplete if the goal of adaptationism is to explain how traits actually evolved, precisely because it concentrates on the final state and not the process that moves it there.

Perhaps Orzack and Sober do not intend (O) to be a statement about actual evolutionary trajectories. Perhaps (O) and its generalization (A) represent claims that the world is as if natural selection were the only causal process operative in evolution. In that case, the above criticisms are irrelevant, but insofar as evolutionists see themselves as concerned with the processes that actually cause evolutionary change, these "as-if" hypotheses are not very relevant or interesting. Moreover, passages from Orzack and Sober's article seem to indicate that they share our view that (O) is actually a historical claim. For example, they claim (p. 367) that an evolutionarily stable strategy (ESS) "is evidence that natural selection has produced a locally optimal phenotype."

The second ambiguity in (O) concerns the backward time scale of the censored models. Are these models supposed to take us from a few generations prior to the observation, or from a hundred, a thousand, or a million generations? How this question is answered matters for at least two different reasons.

First, some ESSs can become fixed in a population by natural selection alone, once the ESS genotype is at a high enough frequency, but at lower frequencies selection will not take it to fixation (see, e.g., Rausher 1984; Rausher and Englander 1987; we will discuss this example in the next section). Thus, from a shorter-term perspective, (O) will be true of this trait, but from a longer-term perspective it will be false. In cases such as this, to evaluate (O) we need to know how far back in generational time we are to start our censored model.

Second, it is generally conceded that natural selection cannot, and is not supposed to, explain the initial appearance of any variant; natural selection can only explain the relative success of different variants in competition with one another. Therefore, again it matters how far back we start our explanatory model. If we go back far enough, the trait *T*, whose fixation we are trying to explain, will not yet exist in the lineage. In that case, something beyond natural selection, presumably some developmental biology and perhaps some molecular genetics, will be needed. This is not a nit-picking point—it is precisely what is at issue in many contemporary criticisms of adaptationism (e.g., Gould and Lewontin 1979). Put another way, natural selection will be a sufficient explanation of all, or most, of evolution only if all possible variants eventually come to exist. If not, if there are significant biases in the production of variation, then something beyond natural selection will be needed in complete evolutionary explanations. By not giving

any indication about how far back they intend their censored models to extend, Orzack and Sober effectively evade this controversy. But evading is not resolving.

PROPOSITION (O) IS A CONJUNCTION OF TWO INDEPENDENT CONDITIONS

The ambiguities discussed above can be resolved, and we do so below. But our major criticism of (O) has to do not with its ambiguity or vagueness, but rather with the confusions that result from the conjunction of (1) the idea that natural selection is the sufficient, or sole, cause of *T* with (2) the idea that *T* is optimal. These two ideas are logically, and biologically, quite distinct, and neither implies the other. However, we will show that Orzack and Sober conflate them at several crucial places in their argument.

Proposition (O) is a conjunction of the statements “Natural selection is a sufficient explanation of the evolution of *T*” and “*T* is locally optimal.” For the sake of this discussion, and for reasons outlined in the previous section, let us resolve the ambiguities inherent in the first part (conjunct) of this conjunction by interpreting it as follows:

- (S) Natural selection is the sole process involved in the evolution of *T* (from the point in time at which all of the relevant variants exist in the relevant lineage). (S stands for selection.)

Let us label the second conjunct of their proposition (O) as (O*):

- (O*) *T* is locally optimal.

Although we are not sure that Orzack and Sober would agree, we see (S) as a more precise and defensible version of the first conjunct of their (O), and we are thus interpreting (O) as the combination of (S) and (O*). By specifying that natural selection is the *sole* process causing evolutionary change, this criterion avoids the ambiguities inherent in the notions of “sufficient explanation” and “only important cause.” We later examine the consequences of relaxing this aspect of criterion (S). (Note that [S] logically fits the series starting with [U] and [I]. That is, [S] entails [I], but not conversely, and [I] entails [U], but not conversely. The conjunct [O*] is logically irrelevant in this series of hypotheses of increasing strength.)

The first point we want to make is that (S) and (O*) are independent of one another, that is, (S) does not imply (O*) and (O*) does not imply (S). The first half of this, that (S) does not imply (O*), is clear. There are numerous situations in which natural selection can be the sole evolutionary process in operation but in which a locally optimal phenotype will not evolve to fixation. Particularly interesting in this context are cases of negative frequency-dependent selection, that is, cases where the rare phenotype or genotype is at a selective advantage precisely because it is rare. An example that is plausibly quite general is negative frequency dependence that results from host-parasite coevolution (May and An-

derson 1983; Seger and Hamilton 1988). Differential resource utilization can also yield negative frequency-dependent selection (Wilson and Turelli 1986), as can inbreeding avoidance, as in the evolution of incompatibility systems (Charlesworth and Charlesworth 1979). Brandon and Antonovics (1995) present a general model of organism-environment coevolution that subsumes many of these sorts of negative frequency dependence. In that model, the locally optimal genotype can never evolve to fixation. We could easily expand this list of cases, but suffice it to say that we need not look to biologically obscure and rare examples to see that (S) does not entail (O*). Orzack and Sober clearly recognize this point, but that recognition does not seem to affect the logic of their argument.

That (O*) does not entail (S) may not be equally obvious. However, theoretical analyses have revealed that there are biologically important characters for which the optimal phenotype or genotype, the ESS, cannot evolve by selection alone. (This is the example alluded to in the preceding section.) Cases involving the evolution of sex ratios and habitat selection, examples Orzack and Sober take as paradigms for testing adaptationism, illustrate this phenomenon.

In the evolution of habitat selection under soft selection, the ESS is to allocate offspring to two habitats in proportion to the numbers of individuals each habitat contributes to the mating pool. A homozygous genotype that does this is truly an ESS because no other alleles are capable of invading (Rausher 1984). However, if the system begins with the "optimal" allele absent, it will equilibrate at a stable polymorphism that is an evolutionary stable state (*sensu* Orzack and Sober). At this point, if the optimal allele is introduced, it will not actively invade—natural selection does not actively favor the ESS genotype. Rather, the new allele will coexist with the others in a neutrally stable state (Rausher and Englander 1987). Genetic drift and other disturbing processes will perturb the system from this neutral equilibrium, and selection will then return it to another neutrally stable state, usually with different gene frequencies. This combination of drift and selection may eventually lead to the fixation of the optimal allele—the evolution of an ESS—but selection by itself will not cause it to happen. The operation of genetic drift is also required. Therefore, (O*) would be true here, but not (S). Eshel and Feldman (1982) demonstrated that sex-ratio evolution behaves in the same way. The common feature of sex-ratio and habitat-selection evolution is that two or more groups of individuals, membership in which is at least partly determined genetically, contribute fixed proportions of individuals to the mating pool. It is likely that other biological situations in which this condition is met will also be characterized by ESSs whose evolution requires drift, or some analogous process, in addition to natural selection.

The propositions (S) and (O*) are thus logically and biologically independent; neither implies the other. This independence should not be surprising. Proposition (S), as we have phrased it, is essentially a historical statement. It makes a claim about the processes that actually occurred to cause a population to evolve to some state. By contrast, (O*) is a statement concerning the current state of the population; insofar as it is a statement about processes at all, it is about processes currently operating to maintain the population in its present state, that is, about processes that prevent invasion of the ESS by alternative alleles. Yet, there is

no reason to believe that evolutionary processes that initially created a character are necessarily the same ones that prevent it from changing or breaking down. As stressed by Maynard Smith (1978) and Crow (1988), the evolution of meiosis and sexual production provides an illustrative example. Sexual reproduction may have originally evolved as a mechanism for mutational repair (Bernstein et al. 1984) but may be maintained in many species primarily because it increases average offspring viability in a variable environment (Bulmer 1980).

Why does this matter? It matters because in order to test a hypothesis of the form (P and Q), where (P) and (Q) are logically independent, one must test the conjuncts (P) and (Q) independently. In particular, to confirm (P and Q) one must confirm (P) and (Q) separately, otherwise a serious fallacy is committed. For instance, the observation of green grass should not be taken as confirming evidence of the conjunctive hypothesis "God exists and grass is green"; nor should the observation of a sunny day be taken as confirming evidence of the logically contradictory hypothesis "It is raining and it is not raining." But, as we will show in the next section, Orzack and Sober confusingly intertwine (S) and (O*) in a way that leads them to commit just this fallacy.

CRITIQUE OF ORZACK AND SOBER'S TEST OF (O)

In setting out their statement of (O), Orzack and Sober say, "We define the concept of sufficient explanation by reference to the predictions one obtains from a 'censored' model (i.e., a model in which the only evolutionary force is natural selection)" (p. 363). Notice that this definition says nothing about optimality. Optimality models are, they say, a kind of censored model (implying that nonoptimality models, presumably straightforward population genetic models that include natural selection as their only evolutionary factor, are also of this kind). They then say, "If the predictions of this [censored] model fit the observations in a statistical sense . . . , (O) can be regarded as true" (p. 363). But this is taking evidence for what we are calling (S), that selection is the sole operative evolutionary factor, and concluding from it (O), which includes as a conjunct (O*). But as shown above, this is a logical fallacy unless (S) implies (O*). And, (S) clearly does not.

In the section entitled "Evolutionary Stable Strategies and States," Orzack and Sober make the opposite mistake. There they take evidence that a trait is locally optimal, that is, is an ESS, making (O*) true, as confirmation of (O), which, of course, contains (S) as a conjunct. According to them, "An evolutionarily stable state and an ESS differ significantly in their implications as to the power of natural selection" (p. 366). An evolutionarily stable state (not [O*]) only indicates that natural selection has been important (I), whereas an ESS ([O*]) "is evidence that natural selection has produced a locally optimal phenotype. Accordingly, the distinction between state and strategy parallels the distinction between (I) and (O)" (p. 367). But again this inference is a logical fallacy unless (O*) implies (S), which, as shown above, it does not.

This last mistake seems to pervade Orzack and Sober's article in that their basic message is that optimality models, when properly constructed, can be used

to test (O). In particular, in claiming that tests of optimality models constitute an appropriate test of adaptationism, the authors argue, "If an optimality model proves to be quantitatively accurate with respect to its prediction of the population and individual phenotypes . . . , then it is appropriate to conclude that the trait is optimal; that is, (O) can be reasonably regarded as true" (p. 370).

We conclude that because of their failure to disentangle questions about current optimality from questions about historical evolutionary mechanisms, their failure to separate (O*) from (S), Orzack and Sober's suggested method for testing adaptationism is thoroughly flawed. Following their suggested method would tend to result in false confirmations. (Taking evidence for statement [P] as confirming the conjunction [P and Q] is this sort of false confirmation.) That is, their method is structurally biased in favor of the hypothesis of adaptationism, (A). We have no reason to think Orzack and Sober intended this; rather, we think that this is an unintended consequence of their conflation of (S) and (O*).

GENETIC VARIATION FOR A TRAIT: WHAT INFERENCES CAN ONE DRAW?

A related issue is the question of what phenotypic variation among individuals implies about both optimality and adaptationism. Orzack and Sober (p. 369) argue that "if the model predicts a set of phenotypes, one must determine whether an individual manifests (or can manifest) the predicted set of phenotypes. A necessary condition for acceptance of (O) is that there be no significant differences among individuals in the fit of their phenotype(s) to the prediction(s)" of an O-type model (Orzack and Sober's criterion for "significant differences" among individuals is that there is genetic variation for the trait in question.) Although we find the authors' discussion (pp. 370–373.) of this issue difficult to understand, they seem to be arguing that there is no general reason for expecting adaptations to exhibit genetic variation and that therefore any genetic variation among individuals should be taken as evidence for the rejection of (O).

Although we would not maintain that there are no optimal traits that lack genetic variation, three problems with Orzack and Sober's argument militate against using the absence of genetic variation for a trait as a criterion for adaptation or optimality. First, there are cogent theoretical reasons for believing that traits under selection should exhibit some variation. In particular, traits subject to stabilizing selection are expected to exhibit variation due to a balance between selection on the one hand, and mutation and recombination on the other (Lande 1975; Hill 1982; Rice 1988). Because mutation is a universal phenomenon affecting virtually all traits, we can expect that for most traits there will be some genetically based variation among individuals, even if there is an optimal phenotype. To require the complete absence of (genetic) variation in a trait in order to conclude the trait is optimal therefore seems theoretically to constitute a strong bias against concluding that, in general, traits are optimal or adaptive. In addition, Orzack and Sober's argument does not consider situations in which several phenotypes (and their associated genotypes) may have the same, maximal fitness independent of frequency and thus may be selectively neutral. We see no reason to believe

that an optimality model could not produce such a set of phenotypes, which could coexist in a population.

Second, it is well established empirically that most traits that have been examined in detail genetically, including those linked directly to components of fitness, are genetically variable in natural populations (Istock 1983; Falconer 1989). By Orzack and Sober's criteria, this evidence would indicate that, in general, the thesis of adaptationism is false and would render any further tests of adaptationism unnecessary. Rather, it makes more sense to us not to reject an O-type model if the amount of genetic variation in a trait is consistent with what is expected from mutation. Although this requires knowledge of the mutation rate for a character, in principle such mutation rates can be obtained experimentally (Mukai 1964; Mukai et al. 1972; Houle et al. 1992). We believe that this approach is much more in accordance with what evolutionary biologists would consider "optimality" than the criterion suggested by Orzack and Sober: natural selection essentially produces an optimal phenotype, except for a little variation around the optimum inevitably introduced by mutation. (Here we have focused on mutation, but similar remarks could be made about recombination, migration, developmental "noise," and other factors producing population-level genotypic or phenotypic variation.)

Finally, even if one is, using this broader criterion, able to falsify an optimality model by showing that there is more variation than can be accounted for by mutation rates, it does not necessarily follow that natural selection was not the sole process responsible for the evolution of the trait in question, especially since under many types of selection genetic variation is expected. In other words, genetic variation does not imply that a particular trait is not an adaptation, if adaptation is taken to imply something about the evolutionary history of the trait (see, e.g., Brandon 1990).

TESTING (O*) AND (S)

Having delineated (O*) and (S) as components of (O), we can now ask whether these propositions are testable. Consider first (O*). Applied to a particular trait in a particular population, we suggest a modification of Orzack and Sober's criterion for whether a trait is optimal: first determine whether the mean value of the trait in the population is as predicted by the optimality model; second, determine whether the amount of genetic variation for the trait is consistent with that expected from an estimate of the mutational variance.

Two caveats must be added to a criterion of this sort. First, if one finds that the mean of the trait differs from that predicted by an optimality model, there are two possible explanations: either (1) the optimality model is not appropriate or (2) the model is appropriate, but the population is not at equilibrium and has not yet converged to the optimum. These two explanations have opposite implications for whether we believe evolution produces optimal traits. In many cases, particularly those in which some genetic variation is present, it should be possible to distinguish between these two possibilities by measuring the adaptive landscape for the trait (e.g., Lande and Arnold 1983; Rausher 1992). In case 2,

the measured fitness surface should be similar to that predicted by the optimality model, whereas in case 1 it should be different.

Second, in many situations the optimal value of a trait depends on context. For example, in some models of local mate competition, the optimal brood sex ratio depends on factors such as the spatial distribution of females, variance in female fecundity, and the amount and kind of information about group size that is available to an individual (Stubblefield and Seger 1990), such that different individuals may have different optima. In these types of situations, determining whether a trait is optimal will require determining (1) whether the norm of reaction, across all relevant contexts, is in accordance with that predicted by the optimality model under consideration and (2) whether the amount of genetic variation associated with the norm of reaction is consistent with that expected from estimates of mutational variance and covariance.

Can (S) be tested? Proposition (S) is a historical statement about the evolution of a trait. It is, in particular, a statement about the processes that are responsible for moving a population from state A to state B. In its most extreme form, it states that natural selection is the sole process responsible for the evolution of the population from state A to state B. As a generalization about the process of adaptation, we know that this extreme form is almost certainly false. We know, for example, that genetic drift operates in all populations because all populations are finite. We also know, from many studies of natural populations, that gene flow and genetic constraints frequently affect the trajectory of evolutionary change.

However, as a thesis of adaptationism, this extreme form of (S) is probably too stringent. Rather, a more appropriate form would be the statement that (S) is true if it is primarily selection that has moved a population from state A to state B. Other processes may affect the detailed trajectory of the population, but if these processes could be eliminated, selection would still cause the population to move from state A to state B, albeit along a somewhat different trajectory.

This idea may be formalized in the following way. Consider the set of possible models that account for the evolution of a population from state A to state B. Each model may contain one or both of two kinds of factors: (1) a pattern of selection, which we designate by s , and (2) a set of other processes, such as genetic drift, migration, genetic constraints, and so forth, that act in a particular way and that are designated collectively by f . We say that selection is "primarily responsible" for the evolution of the population, that is, (S) is true, if the model most consistent with observations has the following property: removal of the factors f from the model but keeping the same pattern of selection, s , produces a model that also moves the population from state A to state B. If removal of f from the model causes the population to move to a different state, then clearly factors other than selection are needed to explain the net evolutionary trajectory, and (S) should be rejected.

Even this form of (S) may be too extreme for the thesis of adaptationism. In particular, consider a population in which a new advantageous mutation arises. Selection by itself would be expected to fix this allele, that is, move the population from $p = 0$ (state A) to $p = 1$ (state B'). However, because of mutation restoring the old allele, the actual trajectory of the population is expected to be from $p =$

0 to some value of p slightly less than 1 (state B). Using the above criterion, then, we would conclude that (S) is not true. The best model contains selection (s) and mutation (f). Removal of mutation does not produce a model that moves the population from state A to state B. However, since B' is very close to B, the model with just selection "essentially" explains evolution from state A to state B. We believe that most evolutionary biologists would consider the almost-fixation of an advantageous allele to be an example of adaptation.

This argument thus suggests an even less stringent criterion for acceptance of (S), one that we believe captures the essence of what most evolutionary biologists mean by "adaptation": choose among all possible models that describe the observed evolutionary trajectory (state A \rightarrow state B) the one that best fits observations. If the pattern of selection in this model by itself will cause the population to evolve from A to a state very close to B, then (S) is true. Of course, just what one means by "very close to B" is somewhat arbitrary. We believe, however, that this simply reflects an inherent arbitrariness concerning what adaptationism is taken to mean.

We recognize that strict application of this type of criterion necessitates identification of all possible models that can move a population from state A to state B, and that this may be in many cases an impossible task. There will be, after all, an infinite number of possible models. There is thus some question as to whether in principle (S) is testable. However, we believe that in many cases there is likely to be a manageable set of plausible models. The goal of the investigator is then clearly defined: evaluate the relative match of the parameters, assumptions, and predictions of these models to the results of observations and experiments. In particular, accepting (S) requires showing not only that a model involving only selection captures the "essence" of the observed evolutionary change, but that other models that require other, nonselective factors do not.

We conclude that (S) is in principle testable for individual cases, even though in many cases it will prove practically impossible to test. If one is interested in the general thesis of adaptationism, however, one needs to test the generalization of (S). We would state this generalization as follows: For most traits in most populations, the evolutionary trajectory resulting in the current state of the trait from some initial state has been governed principally by natural selection. How can this generalization be tested? Orzack and Sober suggest testing their similar generalization of (O) by simply looking at a number, they say 40 or 50 (p. 377), of individual cases to see whether most confirm or disconfirm the individual instances of (O). This is a perfectly sensible procedure, provided that the class governed by the generalization is well enough characterized that one can address the question of how representative the sample used in testing the generalization is. However, the class of all traits is much too poorly characterized for that. We do not pretend to have anything positive to contribute to the question of what is to count as a trait. Nevertheless, there are two ways in which we can at least partially circumvent this problem in the testing of the generalization of (S).

First, if we end up rejecting the generalization of (S), then it is plausible that the above issue is not a problem at all. Unless we define traits as aspects of organisms that directly affect fitness, which strikes us as too narrow a character-

ization, it seems unlikely that empirical population biologists sample the class of traits randomly. That is because they tend to study traits that seemingly have a fairly direct link to fitness. Obviously, (S) is more likely to be true of such traits than of those that seemingly have an indirect or no linkage to fitness. But if our sampling is biased toward those traits that would most likely confirm (S), yet we fail to find confirmation, then we should feel even more confident in our rejection of the generalization of (S).

Second, there is another way of testing the generalization of (S) that largely avoids the sampling problem. Although this generalization has an important historical dimension that is most directly tested by looking at a number of individual instances, as a generalization it deals with all evolutionary processes—past, present, and future. Thus, empirical studies of contemporary populations are relevant to it. They can examine whether current evolutionary dynamics are dominated by selection or whether in explaining the dynamics (of change or stasis), models require the inclusion of factors such as drift, recurrent mutation, gene flow, and genetic constraints. Study of such evolutionary factors is not entirely trait-specific. (For example, gene flow is independent of any particular trait, as is effective population size as it relates to drift. Similarly one can generalize about mutation rates in particular taxa independent of particular traits. On the other hand, meaningful talk of genetic constraints is more likely to be tied to particular traits.) Good work of this sort is admittedly difficult to plan and execute and is highly labor-intensive. But it can be done and so the generalization of (S) can be tested. A considerable amount of relevant data are already in (e.g., the role of gene flow: McNeilly and Antonovics 1968; Barton and Hewitt 1985), enough that we would hazard the educated guess that the generalization of (S) is false. This case is admittedly weak, however, and much work remains to be done.

CONCLUSIONS

We have criticized the attempt of Orzack and Sober to state the thesis of adaptationism and to provide the means for testing it. We have shown that their statement of the adaptationist hypothesis is ambiguous in important, but correctable, ways. Unfortunately, even when made more precise, Orzack and Sober's method for testing it is fundamentally flawed. Their mistake, conflating a hypothesis about evolutionary mechanisms (S), with one about evolutionary products (O*), leads them to recommend a testing procedure that is biased in favor of adaptationism.

In spite of this, we find there is much of value in their article. Their criticism of the literature applying optimality theory seems on target. More to the point of this article, Orzack and Sober's basic idea—to state adaptationism as a testable hypothesis—is, we think, entirely salutary, especially given the centrality of the controversy over adaptationism within contemporary evolutionary biology. We have tried to build on their basic idea by stating two hypotheses, (S) and (O*), that are precise enough to test, and we have shown how they can be tested.

It is interesting that optimality models play little role in testing the thesis of adaptationism. Optimality models could well be used to test particular applica-

tions of (O*), but they can play no role in testing (S) or its generalization, which we believe to represent the core of adaptationism. Without a one-to-one mapping of mechanism onto result, a method that looks only at results could not possibly test a hypothesis about mechanisms. The attraction of optimality models is clear—they allow one to avoid history and genetics. Years ago in a discussion about number theory, Bertrand Russell said, “The method of ‘postulating’ what we want has many advantages; they are the same as the advantages of theft over honest toil. Let us leave them to others and proceed with our honest toil” (1919, p. 71). These are exactly our thoughts with respect to optimality models and the rigorous test of adaptationism.

ACKNOWLEDGMENTS

The order of the authors’ names on this note is alphabetical and has no other significance. We wish to thank J. Seger, G. C. Williams, and two anonymous reviewers whose comments significantly improved the manuscript.

LITERATURE CITED

- Barton, N. H., and G. M. Hewitt. 1985. Analysis of hybrid zones. *Annual Review of Ecology and Systematics* 16:113–148.
- Bernstein, H., H. Byerly, F. A. Hopf, and R. E. Michod. 1984. Origin of sex. *Journal of Theoretical Biology* 110:323–351.
- Brandon, R. N. 1990. *Adaptation and environment*. Princeton University Press, Princeton, N.J.
- Brandon, R. N., and J. Antonovics. 1995. The coevolution of organism and environment. Pages 211–232 in G. Wolters and J. Lennox, eds. *Concepts, theory, and rationality in the biological sciences: the Second Pittsburgh-Konstanz Colloquium in the Philosophy of Science*. Universität Konstanz Verlag, Konstanz; and Pittsburgh University Press, Pittsburgh.
- Bulmer, M. G. 1980. The sib-competition model for the maintenance of sex and recombination. *Journal of Theoretical Biology* 82:335–345.
- Charlesworth, D., and B. Charlesworth. 1979. The evolution and breakdown of S-allele systems. *Heredity* 43:41–55.
- Crow, J. F. 1988. Genetic loads and the cost of natural selection. Pages 56–73 in R. E. Michod and B. R. Levin, eds. *The evolution of sex*. Sinauer, Sunderland, Mass.
- Eshel, I., and M. W. Feldman. 1982. On evolutionary genetic stability of the sex ratio. *Theoretical Population Biology* 21:430–439.
- Falconer, D. S. 1989. *Introduction to quantitative genetics*. 3d ed. Longman, New York.
- Gould, S. J., and R. C. Lewontin. 1979. The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. *Proceedings of the Royal Society of London B, Biological Sciences* 205:581–598.
- Hill, W. G. 1982. Predictions of response to artificial selection from new mutations. *Genetical Research* 40:255–278.
- Houle, D., D. K. Hoffmaster, S. Assimacopoulos, and B. Charlesworth. 1992. The genomic mutation rate for fitness in *Drosophila*. *Nature (London)* 359:58–60.
- Istock, C. A. 1983. The extent and consequences of heritable variation for fitness characters. Pages 61–87 in C. G. King and P. S. Dawson, eds. *Population biology: retrospect and prospect*. Columbia University Press, New York.
- Lande, R. 1975. The maintenance of genetic variability by mutation in a polygenic character with linked loci. *Genetical Research* 26:221–234.
- Lande, R., and S. J. Arnold. 1983. The measurement of selection on correlated characters. *Evolution* 37:1210–1226.

- Lewontin, R. C. 1978. Adaptation. *Scientific American* 239:156–169.
- May, R. M., and R. Anderson. 1983. Epidemiology and genetics in the coevolution of parasites and hosts. *Proceedings of the Royal Society of London B, Biological Sciences* 219:281–313.
- Maynard Smith, J. 1978. *The evolution of sex*. Cambridge University Press, Cambridge.
- Mayr, E. 1983. How to carry out the adaptationist program? *American Naturalist* 121:324–334.
- McNeilly, T., and J. Antonovics. 1968. Evolution in closely adjacent plant populations. IV. Barriers to gene flow. *Heredity* 23:205–218.
- Mukai, T. 1964. The genetic structure of natural populations of *Drosophila melanogaster*. I. Spontaneous mutation rate of polygenes controlling viability. *Genetics* 50:1–19.
- Mukai, T., S. I. Chigusa, L. E. Mettler, and J. F. Crow. 1972. Mutation rate and dominance of genes affecting viability in *Drosophila melanogaster*. *Genetics* 72:335–355.
- Orzack, S. H., and E. Sober. 1994. Optimality models and the test of adaptationism. *American Naturalist* 143:361–380.
- Rausher, M. D. 1984. The evolution of habitat preference in subdivided populations. *Evolution* 38:596–608.
- . 1992. The measurement of selection on quantitative traits: biases due to environmental covariances between traits and fitness. *Evolution* 46:616–626.
- Rausher, M. D., and R. Englander. 1987. The evolution of habitat preference. II. Evolutionary genetic stability under soft selection. *Theoretical Population Biology* 31:116–139.
- Rice, W. R. 1988. Heritable variation in fitness as a prerequisite for adaptive female choice: the effect of mutation-selection balance. *Evolution* 42:817–819.
- Russell, B. 1919. *Introduction to mathematical philosophy*. Allen & Unwin, London.
- Seger, J., and Hamilton, W. D. 1988. Parasites and sex. Pages 176–193 in R. E. Michod and B. R. Levin, eds. *The evolution of sex*. Sinauer, Sunderland, Mass.
- Stubblefield, J. W., and J. Seger. 1990. Local mate competition with variable fecundity: dependence of offspring sex ratios on information utilization and mode of male production. *Behavioral Ecology* 1:68–80.
- Williams, G. C. 1992. *Natural selection: domains, levels, and challenges*. Oxford University Press, New York.
- Wilson, D. S., and M. Turelli. 1986. Stable underdominance and the evolutionary invasion of empty niches. *American Naturalist* 127:835–850.

ROBERT N. BRANDON*

DEPARTMENTS OF PHILOSOPHY AND ZOOLOGY
DUKE UNIVERSITY
DURHAM, NORTH CAROLINA 27708

MARK D. RAUSHER†

DEPARTMENT OF ZOOLOGY
DUKE UNIVERSITY
DURHAM, NORTH CAROLINA 27708

Submitted April 11, 1994; Revised March 28, 1995; Accepted April 7, 1995

* E-mail: rbrandon@acpub.duke.edu.

† E-mail: mdr@mendel.zoo.duke.edu.