How to Formulate and Test Adaptationism

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HOW TO FORMULATE AND TEST ADAPTATIONISM

Although Brandon and Rausher (1996, this issue) are highly critical of our article (Orzack and Sober 1994a), their approach differs little from ours. We find some of their suggestions to be reasonable; others reflect mischaracterization of our arguments in important ways.

In our article and in another previous article (Orzack and Sober 1994b), we suggested that an adaptationist view of a trait T is best understood as the following proposition:

> (O) Natural selection is a sufficient explanation of the evolution of T, and T is locally optimal.

Brandon and Rausher claim that the second conjunct (which they call [O*]) is irrelevant to the issue of adaptationism and that the first should be replaced by the proposition they call (S):

> (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).

However, they state (p. 197) that this form of (S) is almost certainly false and that it should be weakened to say that "selection is 'primarily responsible' for the evolution of the population." Brandon and Rausher go on to say (p. 198) in regard to acceptance of this weakened form of (S) that one should "choose among all possible models that describe the observed evolutionary trajectory (state A → 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."

SUFFICIENT EXPLANATION

Natural selection is a sufficient explanation, according to the definition in our article (p. 363), if a "censored" model in which natural selection is the only evolutionary force makes predictions that are statistically indistinguishable from an "uncensored" model in which all the evolutionary processes at work are accurately represented. This concept makes precise our idea that an adaptationist analysis is one that views natural selection as the "only important cause" of the trait's evolution (p. 361).

Brandon and Rausher claim that our concept of sufficient explanation should be replaced by (S). However, they explain what "primarily responsible" means by comparing a model in which selection and other forces are accurately represented with one in which only selection is represented. If these models make the same or nearly the same predictions about trait evolution, then selection is primarily responsible. This is a slightly weaker version of our notion of "sufficient explanation." Whereas our concept requires the censored and uncensored models to make the same predictions, their concept of primary responsibility requires the two models to make nearly the same predictions. Hence, although Brandon and Rausher criticize the concept of "only important cause" by saying that it is "ambiguous," they embrace basically the same concept (see also Sober 1993).

PROCESS AND OUTCOME

Unfortunately, some of Brandon and Rausher's criticism of the concept of sufficient explanation stems from their mistaken understanding of our claims. They write (p. 190) about our article that "a model involving only natural selection is deemed a sufficient explanation if . . . the model predicts a final state T in a population and observations are, within the limits of estimation error, consistent with this prediction and . . . all individuals in the population exhibit the same phenotype or distribution of phenotypes." On this basis, Brandon and Rausher claim that our test of the optimality of a trait is flawed because it does not account for the distinction between evolutionary process and evolutionary outcome. In essence, Brandon and Rausher misdescribe our test as a statistical exercise in which the *only* component is a comparison of data and predictions. We stated (p. 361) that "a phenotype of an individual is optimal (relative to a variety of alternatives) because it outperforms the other phenotypes and thereby results in a higher fitness." Nothing about this definition restricts it to an equilibrium state. We stressed later (p. 365) that the optimality of a given trait is always to be judged in the context of a specific model. As a result, for example, at least some information on evolutionary dynamics will be available to the investigator. To this extent, we did not advocate separate assessments of process and outcome. If the model deemed most relevant is one in which, say, it appears that a trait can increase from a small frequency only via genetic drift, as later described by Brandon and Rausher (p. 193), then it is obvious that such information should be used in assessing the optimality of the trait. More generally, we stated (p. 364) that "of course, additional considerations may contribute to a decision to accept a claim as to the sufficiency of natural selection even given statistical accuracy of the censored model's predictions." We then described an example of a situation with such "additional considerations," one in which a neutral model and a selective model of trait evolution have exactly the same sampling distribution. Even perfect statistical accuracy would not be enough in this instance to accept the selective model. One should use all available information in assessing the adequacy of a model, including information on evolutionary dynamics.

Brandon and Rausher go on to claim that we give precedence to optimality models relative to other models. They take our statement (p. 363) "if the predic-

tions of [an optimality] model fit the observations in a statistical sense, . . . (O) can be regarded as true" as evidence for this. We regret our formulation of this sentence. But any paper is more than a collection of unconnected sentences. One page later (p. 364), we go on to say that "an optimal explanation of a trait does not have precedence over nonoptimal or nonselective explanations. If competing explanations work equally well, additional data or analyses are needed." This clearly anticipates Brandon and Rausher's apparent criticism (p. 190) 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."

OPTIMALITY AND ADAPTATIONISM

Brandon and Rausher claim (p. 192) that (S) and (O*) are independent; by this they mean that neither logically implies the other. This claim was delineated in our article although, obviously, our presentation was not framed in terms of their concepts, (S) and (O*). For example, we wrote (p. 363) that "evolution driven *only* by natural selection can occur in situations in which there cannot be an optimal phenotype," and we went on to discuss two examples for which one can easily see that (S) is true but (O*) is not.

This leaves open the issue of whether (O*) entails (S). We agree with Brandon and Rausher's further claim that (O*) can be true and (S) false, despite the implication to the contrary in our article. If a trait is the one predicted by an optimality model, it is a separate question as to whether natural selection is a sufficient explanation of the evolution of the trait. Brandon and Rausher are mistaken, however, when they write (p. 192) that (O*) and (S) are "*biologically,* quite distinct" (emphasis added). Deductive logic is distinct from biological evidence. Evidence for optimality *is* often evidence for the sufficiency of natural selection.

Brandon and Rausher make an incorrect general claim about confirmation when they write (p. 194) that "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." Evidence for one of two logically independent propositions can be evidence for the other. For example, let (P) be the proposition that an allele has a frequency between 0.60 and 0.80 and let (Q) be the proposition that the frequency is between 0.61 and 0.81. Propositions (P) and (Q) are logically independent. Yet, it is easy to see how evidence confirming one can also be evidence confirming the other.

Brandon and Rausher claim (pp. 199–200) that "optimality models play little role in testing the thesis of adaptationism. Optimality models could well be used to test particular applications of (O*), but they can play no role in testing (S) or its generalization, which we believe to represent the core of adaptationism." We disagree. An optimality model does more than identify an optimal trait. As noted above, it also describes a selection process that leads to the evolution of this trait. If the observed trait is not the one predicted by the model, this is highly relevant to whether the selection process postulated by the model took place.

The testing of optimality models is central to the question of whether natural selection is the most important cause of what we observe.

EVOLUTIONARY DYNAMICS

Brandon and Rausher's characterization of evolutionary dynamics (p. 193) may suggest to the reader that the processes they describe are general. In fact, they are known not to be. Brandon and Rausher correctly describe the fact that some evolutionarily stable strategy (ESS) models are degenerate in that at equilibrium all traits have the same fitness. The prototypical example in this regard is a Fisherian model of sex ratio evolution in an infinite panmictic population. Neutral trait evolution can occur to the extent that any sex ratio is equally fit as long as the population sex ratio is 1:1 (but see below). However, this dynamical behavior is not typical of extant ESS models. For example, all such models of trait evolution in structured populations are nondegenerate; that is, the models predict that *each individual* manifest the ESS. Such models include those relating to sex ratio evolution, the evolution of altruism, and the evolution of migration behaviors. Nondegeneracy is reflected in the curvature of the fitness surface around the optimum. In the Fisherian model of sex ratio evolution, the fitness surface is flat at equilibrium, which implies that all sex ratios have equal fitness. In a structured population model of sex ratio evolution, the fitness surface is necessarily curved, which implies that nonoptimal sex ratios have lower fitness to a degree dependent upon the degree of population subdivision. Examples of such curved fitness surfaces are shown in Orzack et al. (1991) (although their interpretation of the model in question as degenerate is incorrect). To speak then, as Brandon and Rausher do, of sex ratio evolution as though it is a single process, is misleading (see also Uyenoyama and Bengtsson 1982, pp. 52–54).

Even for traits for which an ESS model predicts degeneracy at equilibrium, neutral trait evolution may not occur in natural populations. As noted in our article (Orzack and Sober 1994a), stochastic perturbations to the payoff matrix and various consequences of the finite nature of populations imply that natural selection may often favor the ESS even when the model strictly implies that neutral trait evolution can occur (Hines 1982, 1990, 1995; S. Orzack and W. G. S. Hines, unpublished manuscript). Our point is that the dynamics of the "neutrally stable state" described by Brandon and Rausher (p. 193) are relevant to understanding trait evolution in particular instances. Their existence, however, cannot be used to rule out a priori the possibility that an optimal trait will evolve solely as a result of natural selection.

THE NATURE OF VARIATION

In our article, we emphasized (p. 375) the importance of understanding the nature of variation among individuals; optimality models do not just predict the population mean but also make claims about what each individual in the population should be doing.

We agree with Brandon and Rausher's suggestion that the mutational variance is a relevant consideration when assessing the optimality of a given trait. None-

theless, there are some serious shortcomings in their discussion of genetic varia-
tion. They claim that "virtually all traits" have genetic variation and, to this
extent, the absence of genetic variation cannot be used as a meaningful criterion
for the assessment of optimality. First, we agree that many published analyses
of traits reveal the existence of genetic variation. However, many do not, and
we suspect that there is a significant bias in this regard, both with respect to the
choice of traits and because many genetic analyses with nonsignificant results are
regarded as "failed," unpublishable experiments. As for the first point, Brandon
and Rausher admit (p. 199) that "it seems unlikely that empirical population
biologists sample the class of traits randomly" and then claim that most traits
studied are more or less closely related to fitness. We do not necessarily agree,
but this is an arguable point. We would add that population biologists studying
genetic variation tend to examine traits with obvious phenotypic variation, this
making the task of determining whether there is genetic variation that much
easier. As for the second point, we have commonly heard questions about statisti-
cal power raised in regard to seminar presentations of analyses in which genetic
variation has not been detected. Both of these filters augment the "frequency"
in the literature of traits that have genetic variation.

Let us imagine, however, that such investigator and publication biases do not
exist and that "virtually all traits" are genetically variable. There is still no neces-
sary contradiction between this fact and the absence or near absence of genetic
variation as a meaningful criterion for the assessment of optimality. The reason
is that for many traits known to be genetically variable, we know only that there
is genetic variation within the species. What is important in the context of testing
the optimality of a particular trait is whether there is genetic variation among the
individuals that interact evolutionarily. The fact that "all traits" exhibit a signifi-
cant response to artificial selection is also ambiguous because in many selection
experiments individuals from more than one area or laboratory strain are used to
form the experiment's base population.

Of course, there are many instances where local, evolutionarily defined popula-
tions are known to be genetically variable. For example, Brandon and Rausher
mention Istock's excellent work on diapause in *Wyeomyia smithii*. Unfortunately,
the generality of this kind of result is unclear.

Our point is that only by marshaling the appropriate kind of evidence in regard
to the disposition of genetic variation will we know whether "genetics has gotten
in the way" of the evolution of optimal traits. Invoking the universality of genetic
variation is ambiguous in the present context because it leaves open the configu-
ration of variation. In the context of assessing optimality there is a fundamental
difference between the evolutionary implications of a locus with many common
variants and the evolutionary implications of a locus with, at most, rare variants.
Brandon and Rausher's arguments do not resolve this issue. Of course, the latter
configuration can be compatible with optimality to the extent that an ESS, for
example, is defined with respect to a trait that is not quite fixed in a population.
In effect, in such a situation rare variants in the population keep the system
honest.

Finally, it is relevant to note in regard to the meaning of genetic variation that

we are a long way from having, in Brandon and Rausher's words, (p. 195), "cogent *theoretical* reasons for believing that traits under selection should exhibit some variation" (emphasis added). Theory has no precedence with respect to data in this context and unfortunately, as noted above, there are some serious gaps in our general understanding of the disposition of genetic variation within and between natural populations. For that matter, we lack unambiguous *data* to rigorously support the notion that stabilizing selection is common in nature (Travis 1989).

CONTEXT AND INTERACTION

Brandon and Rausher agree with us and many others that determining the relative importance of selection in the evolution of a trait is an important exercise. They raise several good points in this regard, but perhaps the most important relates to context and interaction. Brandon and Rausher correctly note that "the optimal value of a trait depends on context" (p. 197). The terms *context* and *interaction* are often used to imply that nature is so complex that traits cannot be optimal. Although we are unsure of Brandon and Rausher's views in this regard, this belief is so common that we briefly address it here.

One person's context and interaction is another person's opportunity for perfection. Our point is that the complexity of trait expression or of the environment is not sufficient by itself to imply that natural selection could not create an optimal trait. The best example of this involves one of the important traits underlying human language: grammar, "the mental system that allows human beings to form and interpret the words and sentences of their language" (O'Grady et al. 1993, p. 3). The meaning of all human speech is context dependent and people speak different languages in different communities, but these facts are entirely consistent with the hypothesis that all humans have the same language faculty as specified by a universal grammar (Chomsky 1988). So, despite the prior arguments one could use to conclude that this trait—one having incredibly complex expression—could not be optimal because it "must be" variable across individuals, populations, and environments, it may not be the case. It is a further question if the universal grammar, if it exists, is in fact optimal. Of course, we make no such claim in the absence of relevant models. The general point is that the nature of complex trait expression must be resolved before assessments can even be made about local optimality or the lack thereof.

ADAPTATIONISM AS A GENERAL THESIS

Brandon and Rausher share our interest in having biologists discover whether adaptationism is true. They agree that adaptationism should be viewed as a claim about what is true concerning most traits in most populations. They agree with us that the word "most" raises questions about representative sampling. As we stated in our article (p. 378), this is a problem for a test of adaptationism as we construe it, especially because optimality relates to evolutionarily interacting individuals. What if different populations of the same species support different

conclusions about the optimality of the trait? This is a problem even with the present small number of complete tests of optimality models. The mix of digging and entering behaviors in *Sphex ichneumoneus*—one of apparently only two traits for which published analyses include proper assessment of proposition (O)— appears to be locally optimal in one population but probably is not in another (see Brockmann and Dawkins 1979; Brockmann et al. 1979). As we mentioned in our article (p. 378), there is work to be done on how the probabilistic distribution of traits and clades should be understood (as is true for any exercise in comparative biology). But this uncertainty is no reason to forgo a test of adaptationism. Instead, it is simply a reminder to be circumspect.

THE TEST OF ADAPTATIONISM AND WHY WE NEED IT

In our article we called for an ensemble test of adaptationism with the hope that a central debate in evolutionary biology could eventually be resolved on the basis of evidence, as opposed to remaining an unresolved conflict between two opposing viewpoints. This is still our hope.

Brandon and Rausher agree with us that adaptationism is testable, but they believe that optimality models play no role in this test. They finish by quoting Bertrand Russell on the "advantages of theft over honest toil" and go on to equate the use of optimality models with theft. Russell's point was that problems are not solved by anything less than the hard work of mustering arguments and evidence. We agree completely with the spirit of his comments as applied to the present context: general claims about the role of natural selection in the evolution of traits should be based on data. It violates Russell's maxim to claim that traits "cannot be" optimal and that the formulation and testing of optimality models do not constitute "honest toil." One wonders what Brandon and Rausher think about Brockmann et al.'s demonstration that the mix of reproductive behaviors of females of *Sphex ichneumoneus* appears to be locally optimal in one population. What part of this work fails to be honest toil?

In contrast to Brandon and Rausher's a priori rejection of optimality models, we suggest that these models can be and sometimes have been shown to be sufficient explanations of traits. The test of adaptationism does, indeed, deserve honest toil.

Why do we need a test of adaptationism? What effect would it have on practice? After all, it is not as though the usefulness of optimality models would be lessened if, say, the test outcome indicated that most traits were not optimal. Nonetheless, having some assessment based on an assemblage of tests as to whether such models often provide sufficient explanations of trait evolution cannot fail to be salutary. It could make easier the task of deciding whether discrepancies between predictions and observations are more likely the result of true nonoptimality or of an incorrectly formulated model. Equally as important is the standardization of test protocols that comes with an ensemble test of adaptationism. At present, the large discrepancies among investigators with respect to the criteria by which optimality models are accepted and rejected serve to greatly lessen the biological

significance of otherwise important analyses. Finally, we hope that an ensemble test of adaptationism would bring much needed attention to the how and why of ensemble testing of hypotheses in evolutionary biology and, perhaps as well, renewed attention to a question central to such endeavors: how traits can and should be defined.

CONCLUSION

The main point of our article was that the optimality of a particular trait is testable and that the accumulation of such tests allows one to test the thesis of adaptationism. The essence of this thesis is that natural selection is so powerful a determiner of evolutionary outcomes that nonselective forces may safely be ignored when understanding the local evolution of the trait. We introduced the concept of sufficient explanation in order to clarify this idea. We also stressed the importance of understanding the nature of variation among individuals when testing an optimality model. None of these points is weakened by Brandon and Rausher's comment.

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