Fitness and Explanation[1]

Gregory Cooper

University of Minnesota

1. Introduction

Sustained controversy over a philosophical issue is often times symptomatic of differing commitments at a more fundamental philosophical level. I will argue that two current debates over the foundations of the theory of natural selection are cases in point. Alexander Rosenberg, at times together with Mary Williams, challenges what is becoming received orthodoxy about the foundations of this theory. He argues that the currently popular propensity interpretation of fitness does not legitimize explanations in terms of natural selection, and that furthermore, the biological fields which typically study the ways in which selection pressures originate in the organism/environment complex are not in fact part of the theory of natural selection at all. His foils in the first case are Robert Brandon, John Beatty and Susan Mills;[2] on the second issue he is engaged in debate with Elliott Sober.[3] We will see that, although the controversies are ostensibly about the interpretation of fitness, the issues, at bottom, involve the nature of scientific explanation.

The first section sets out the essentials of what can be called (loosely) the "received view" of the foundations of the theory of natural selection. The next section focuses on the two controversies, revealing the fundamental role played by differing commitments about the nature of explanation. The final section discusses some of the challenges confronting each of the alternatives.

2. Natural Selection: The "Received View"

The foundations of the theory of natural selection have received a great deal of attention from philosophers and biologists alike. Furthermore, there appears to be an emerging consensus, at least with respect to the broad elements of the picture, among the interested parties. The task in this section is to set out the essentials of what is becoming the "received view" of the foundations of the theory of natural selection. I do not mean to imply that those cast as defenders of this position would be in exact agreement with my formulation, however I do believe that the points of disagreement would be minor in comparison with the overall shared conceptual structure.

The "received view," as I am understanding it, can be characterized by the following five theses:

PSA 1988, Volume 1, pp. 207-215

I. The theory of natural selection, appropriately characterized, is in fact a legitimate scientific theory, where legitimacy is a matter of having explanatory potential.
II. Selectionist explanations are not legitimate if fitness is defined in terms of actual rates of reproductive success, or if the only access to fitness differences is via estimates based on actual rates.
III. Fitness is supervenient on a huge, and disparate, range of particular situations involving organisms and their environments.
IV. Fitness is a *propensity* for reproductive success.
V. The *theory* of natural selection must be distinguished from the *principle* of natural selection. Furthermore, the latter is analytic in the sense that it is a consequence of the probability calculus; it is in effect a rule of direct (statistical) inference.

In the remainder of the section I will comment briefly on these five ideas. The goal is to make the position clear; I will not be arguing the issue of consensus in this paper.

The significance of the first thesis is not *that* the theory of natural selection is legitimate, but that the criterion of legitimacy is *explanatory promise*. Philosophers of science have long been in the business of demarcating the scientific from the unscientific, but the traditional, and singularly unproductive, approach has been in terms of some epistemic principle such as falsifiability or "in principle" confirmability. If an explanatory criterion is to be substituted for an epistemic one, it must be recognized that this puts a burden on one's theory of explanation; in particular, it presupposes that the theory is able to pick out some objective explanatory virtue as a measure of explanatory success.

Thesis II refers to the explanatory circle which has for so long bedeviled the theory of natural selection. If the central claim of the theory is that "the fit survive", then "the fit" better not be defined as "the survivors." Clearly, such a view explains nothing, and since the point has been made repeatedly in the literature, I will not dwell on it here.

The supervenience of fitness is also, by now, widely recognized.[4] Organismic fitness is, in some sense, a measure of an individual organism's ability to survive and reproduce in a given environment. It depends, then, on both the properties of the organism and the properties of the environment. Obviously, different kinds of organisms have different properties, and the features of the environment causally relevant to survival and reproductive success will differ accordingly. To use Sober's example, it would be surprising indeed if the fitness of a cockroach and the fitness of a zebra were to have the same physical basis.

Thesis IV, the propensity interpretation of fitness, was first presented in papers by Brandon (1978) and Mills and Beatty (1979). The idea is essentially that fitness should be understood as the expected contribution of offspring to future generations in a particular environment (in some appropriate sense of "future"). The expectation is arrived at by summing the possible offspring contributions weighted by the probability of their occurrence. Understood in this way, fitness is a measure of an organism's disposition to have a certain degree of reproductive success, rather than, as has sometimes been urged, its actual reproductive success. We have already seen that fitness had better be something other than actual reproductive success; the received view satisfies this constraint by making fitness a probabilistic disposition.

Finally, we come to the distinction between the theory of natural selection and the principle of natural selection. There has probably been more debate over the cognitive status of evolutionary theory, and natural selection in particular, than any other aspect of the theory. Why has it been so tempting to view this theory as lacking empirical content? Because, so the received view says, the central proposition of the theory, the principle of

natural selection, *does* lack empirical content (at least empirical biological content). As Brandon puts it: "What is the structure of evolutionary theory [i.e. the theory of natural selection]? I have presented the following answer: At its core is the principle of natural selection. This principle has no biological content yet still is the most important part of the theory." (1981, p. 438)

When linked with the propensity interpretation of fitness, it is not hard to see why the principle of natural selection is virtually analytic. The principle says, in effect, that for organisms **a** and **b**, if **a** is fitter than **b** (in their common environment), then **a** will probably contribute more offspring than **b** (in that environment). Plugging in the propensity definition one gets: If **a**'s expected offspring contribution is greater than **b**'s (in their common environment), then **a** will probably contribute more offspring than **b** (in that environment).

This is the received view as I understand it. Is it a consistent position? This is a matter of controversy and it is to two such controversies that we now turn.

3. Challenges to the Received View

The previous section closed on a rather curious note. As Brandon put it, at the core of the theory of natural selection is a principle with no biological content. How can a conceptual truth be the "most important part" of the what is commonly regarded as the premier theory in biology? Our first challenge begins with this question.

One prominent advocate of an explanatory criterion of scientific legitimacy was Ernst Nagel. He writes that "...it is the organization and classification of knowledge on the basis of explanatory principles that is the distinctive goal of the sciences." (Nagel 1961, p. 4) But the principles Nagel is talking about are not logical principles. It is by virtue of their effort to capture laws of nature that theories acquire explanatory potential. We must look more closely at where, on the received view, the explanatory promise of the theory of natural selection is to be found.

The following two passages from a paper by Brandon and Beatty are instructive. Concerning the source of biological content they write:

> We both construe Darwinian evolutionary theory [the theory of natural selection] as providing a schema for generating "instantiations" or "applications" of the theory. (These "instantiations" are specific ecological models which may draw on theories from many diverse fields.) And we agree that the empirical biological content of Darwinian evolutionary accounts lies in these instantiations or applications ...rather than in the schema itself. (1984, p. 343)

Of course if these applications are to play an explanatory role, the empirical content must also have explanatory punch. As previously noted, it is here that the propensity interpretation of fitness comes into play:

> Inasmuch as the connections between an entity's dispositions or abilities and its actual behaviors are causal connections rather than analytic connections, the propensity interpretation of 'fitness' allows for genuinely explanatory accounts of differential reproduction in terms of differential fitness. (1984, p. 343)

Thus, particular instantiations give the theory of natural selection biological content, and the dispositional nature of fitness reveals how this content can have explanatory value as well. The actual reproductive success achieved in a certain situation is illuminated by revealing the underlying disposition for reproductive success in that situation.

The most apparent problem with this solution is that propensities, in and of themselves, do not seem suited for the job they are being asked to do. If a rare phenotypic variant is disposed (probabilistically) to go to fixation in a population but in fact goes to extinction instead, in what sense did the disposition *cause* the actual fate of the phenotype? In what sense does it *explain* the actual fate? To the extent that there are causal connections between dispositions and actual behaviors, the relationship would seem to be something like the following. The same kinds of causal factors which comprise the underlying basis for the disposition are responsible for the actual behavior as well. Likewise, the explanatory potential of dispositions is parasitic on the extent to which we understand the underlying basis of the disposition. The upshot is that, on the received view, the explanatory promise of the theory of natural selection appears to rest rather squarely on the "specific ecological models" which are supposed to account for the ways in which fitness differences are generated in the interaction between organisms and their environments.

We are now in a position to state Rosenberg's complaint about the propensity interpretation of fitness. We have seen that for the propensity view to ground the explanatory legitimacy of the theory of natural selection, there must be independent access to that complex set of causal relations involving the organism and its environment which forms the underlying basis of the probabilistic disposition. However, given the supervenience of fitness, the underlying basis will differ from case to case. Suppose we have two different kinds of organisms with the same level of fitness, but with completely disjunctive supervenience bases. In what sense do these organisms have the *same* property? On the propensity interpretation of fitness, these organisms share the same disposition toward reproductive success. But to attribute the same dispositional property in the face of completely disjunctive underlying bases is, it appears, to sever the connection between the disposition and the conditions which give rise to it. This, in essence, is Rosenberg's complaint.

According to Rosenberg, the propensity interpretation at best provides a kind of definitional schema. "Fitness" as it occurs in the general statement of the theory is a placeholder which gets instantiated in different ways in different applications. But because there is no common element to these various instantiations, "...the propensity interpretation does not provide a definition of fitness in any real sense." (Rosenberg and Williams 1986, p. 416). That is, it does not provide a definition which certifies the explanatory virtue of the theory of natural selection.

We can now begin to see two quite different pictures of what it takes to establish explanatory legitimacy. Contrary to Rosenberg, explanatory virtue for Brandon and Beatty does not presuppose that the theory of natural selection be expressible as a set of nomological generalizations. In fact, the explanatory work to which the theory is put need involve neither generality nor nomic force. The biological content may be limited to applying the theory in particular situations and, as Beatty (1980, p. 554) points out, even here "...the empirical instantiations need not be lawlike to play an explanatory role."

For Rosenberg, on the other hand, the explanatory potential of the theory of natural selection hinges on preserving the lawlike character of the theory. If fitness is to be explicated, it must be done in a way which is faithful to that constraint. Since the propensity interpretation is the expectation of reproductive success given the selection pressures at work, it will succeed only if there are lawlike regularities about the ways in which selection pressures originate in the interactions between organisms and their environments. However, owing to the supervenience of fitness, there are no such regularities about sources of selection pressures (at least none that we can formulate). In short, the problem with the propensity interpretation as a means to ground the explanatory virtue of the theory of natural selection is that " ...there are no "evolutionary source *laws* "—discoverable and

manageable nomological generalizations about the universal determinants of fitness." (Williams and Rosenberg 1985, p. 744)

What does this imply about the cognitive status of the theory of natural selection? If (1) the key term in the theory—fitness—cannot be interpreted in such a way as to preserve the lawlike character of the theory, and (2) the theory is explanatorily significant only if it has a lawlike component, then the obvious alternative is to treat fitness as an uninterpreted term. This is what Rosenberg (following Williams) does. In effect, he rescues explanatory potential by denying thesis V—the distinction between the theory of natural selection and the principle of natural selection, and the analyticity of the latter. On the received view, the principle contains the general component of the theory. However, given the propensity interpretation, this generality is a bit too strong—it is analyticity. In rejecting the propensity interpretation, Rosenberg is able to treat the generality associated with the principle of natural selection as nomic rather than logical.[5] On this view, the distinction between the principle and the theory collapses because the "specific ecological models" which, on the received view give the theory of natural selection explanatory content, now become applications of the theory—which has explanatory merit by virtue of its expression of a law of nature.

This brings us to our second controversy. Elliott Sober advances two central criticisms of Rosenberg's position, both connected with his denial of thesis V. To begin, he argues that taking fitness as a primitive term, as Rosenberg does, is not the way to establish the cognitive legitimacy of the theory of natural selection. As he points out, "Even if 'fitness' were a primitive, it still might be analytic or a priori that the fit tend to outsurvive and outreproduce the less fit, in which case all the old tautology conundrums would remain to be resolved." (1987, p. 223)

Furthermore, by taking such a restricted view of the theory (i.e. collapsing the distinction between the principle and the theory), Rosenberg is turning major fields of biological inquiry, such as evolutionary ecology and population genetics, into so much applied biology. Instead of being legitimate theoretical investigations in their own right, these endeavors become exercises in applying the theory of natural selection to the biological idiosyncrasies of our planet.

Sober's alternative involves distinguishing two ways to legitimize a scientific concept (and thereby the explanatory potential of scientific theories expressed in terms of that concept). He claims, "One can legitimize a concept (1) by displaying its connections with concepts that apply at a lower level of organization or (2) by showing how it is connected with concepts that apply at the same level. Call these the vertical and horizontal methods respectively." (1984b. p. 166)

Rosenberg is demanding, unreasonably on Sober's view, that fitness be grounded vertically in laws about how the organism/environment complex generates fitness differences. The supervenience of fitness does indeed prevent this. The alternative is to "ground" fitness horizontally by showing how it is connected with other supervenient properties at the same level of organization. In effect, Sober is attempting to turn supervenience from a vice into a virtue. The regularities which underwrite the explanatory virtue of the theory of natural selection—for example, the source laws for natural selection—only show up in the theoretical constructions which use supervenience to abstract away from the details of particular situations. In Sober's words,

> ...The fact that fitness is a supervenient property was used to argue that there are some explanatory problems in which fitness has an irreducible and unique explanatory utility. The physical bases of fitness are just as explanatory as fitness itself when selection processes are looked at one at a time. But if the point is to explain what physically distinct selection processes have in common, fitness pro

> vides a perspective that fine-grained physicalistic description does not. (Sober 1984b, p. 84)

Thus, Sober agrees with Rosenberg on the central premise—there are no lawlike regularities involving the physical sources of selection pressures. But, for Sober, this means we must look for regularities at a different level of organization; we must construct theories in terms of supervenient properties. The virtue of such theories resides not in clustering phenomena in terms of physical similarities, but in terms of similarities at this supervenient level.[6]

Summarizing then, we have seen that Rosenberg accepts theses I-III, and that, together with his views on explanation as a criterion of scientific legitimacy, this puts him at odds with Brandon and Beatty over thesis IV. The explanatory circle cannot be broken case by case, hence the propensity interpretation of fitness must be given up. Rosenberg's solution, taking fitness as a primitive term, in turn puts him at odds with Sober over thesis V. True the explanatory circle cannot be broken case by case, but we can, on Sober's view, use supervenient properties to capture what the cases have in common.

Thus, differing intuitions about the nature of explanation are playing a central role in these controversies. At issue in the debate over the propensity interpretation is the extent to which subsumption under a law is a necessary condition for explanation. Sober and Rosenberg, on the other hand, disagree about the *kinds* of laws that can function in a scientific explanation. Rosenberg's vertical requirement entails, in effect, that the laws in question must be about (physical) causal mechanisms. Sober argues for an explanatory virtue for supervenient theory which involves abstracting away from the causal details (see Sober 1983). In the final section we will take a brief look at some of the problems facing each of these three approaches.

4. Explanation: the Alternatives

With increasing frequency, the theory of natural selection, and evolutionary biology generally, is being associated with the semantic view of theories (Beatty 1981, Thompson 1983, Lloyd 1984, Waters 1986). As Waters (1986, p. 222) points out, on this view the theory of natural selection is treated "...as a definition of a kind of biological system, rather than as a set of empirically testable laws." The definition of the system itself is without biological content; the content comes by way of empirical hypotheses to the effect that this or that real situation is a model of the theory. An important advantage of the semantic view, so the claim goes, is that it is able to accommodate the explanatory applications of general biological theories without being committed to the (questionable) existence of the fundamental biological laws of nature which, on the more traditional view, these theories are thought to express. But how do theories play an explanatory role on the semantic view?

Since, on this approach, the biological content is contained only in the empirical claims made on behalf of the theory, it is here that one must look for explanatory import. According to Beatty,

> Such empirical claims provide the explanatory link between the nonempirical theory specifications and the behavior of empirical systems. For having identified an empirical system as an instance of a specified kind, an investigator can then account for aspects of the behavior of the empirical system in terms of the consequences of its being an instance of the specified kind. (Beatty 1981, p. 400)

This seems simple enough. In fact, it seems disconcertingly simple.[7] How does it advance our understanding to be given a definition of a formal structure and then informed that the real world is a model of this structure? This is a difficult issue and cannot be

tackled here. It must suffice to point out that (1) the most well developed theory of explanation associated with the semantic view of theories is van Fraasen's (1980) pragmatic approach, and (2) pragmatic theories of explanation are ill-suited to supply the kind of objective explanatory virtue needed for an explanatory criterion of scientific legitimacy.

While the received view of natural selection is prepared to countenance explanation in the absence of laws, but has no theory ready to hand for how such explanation might be possible, Rosenberg, has pretty much the opposite problem. His views on explanation are clearly within the venerable tradition of covering law theorists, but in order to secure explanatory clout for the theory of natural selection he is forced to make two rather strained moves. First of all, he needs a law. So that the principle of natural selection might fill the bill, he makes the somewhat unhelpful move of treating fitness as a primitive term. In addition, he is forced to deny that major portions of theoretical biology (e.g. population genetics and evolutionary ecology) meet "...reasonable criteria for being scientific theories..." because they cannot "...be expected to produce general laws that manifest the required universality, generality and exceptionlessness." (Rosenberg 1985, p. 219).

Sober's solution is to be more liberal about the kinds of laws which can certify explanatory legitimacy. The nature of these laws, and Sober's views on explanation generally, are beyond our scope. I can only point out that (1) for Sober, fitness, owing to its supervenience, is not a physical property, thus (2) the laws of nature in question are presumably not physical laws. The construction of theories in terms of supervenient properties is part of a general methodological strategy which Sober calls "population thinking."

> The heart of population thinking, then, is a commitment to the methodological fruitfulness of constructing theories whose parameters apply to *populations*. It is not, I would suggest, best understood as an ontological thesis about the reality—existence or causal role—of much of anything. (Sober 1984b, p. 168)

I have little quarrel with the methodological fruitfulness of this strategy. But if it is in fact a source of objective explanatory virtue, it is, like it or not, a thesis with ontological commitments. Calling these supervenient regularities "laws" does not, of itself, establish explanatory legitimacy. A further question remains. What is it about these non-physical laws that allows them to function as explanatory principles?[8]

Notes

[1]I would like to thank John Beatty and James Hawthorne for their many helpful comments on earlier versions of this manuscript.

[2]The relevant succession of papers is Brandon (1978), Mills and Beatty (1979), Rosenberg (1982), Brandon and Beatty (1984) and Rosenberg and Williams (1986).

[3]The references for this discussion are Rosenberg (1983), Sober (1984a), Williams and Rosenberg (1985) and Sober (1987).

[4]For a detailed treatment of the supervenience of fitness see Rosenberg (1978).

[5]Rosenberg does not talk of the "principle of natural selection"; his analogue for the received view's "principle" is Williams' (1970) axiomatization, in particular, her axiom D4.

[6]Sober has three kinds of arguments for this unique explanatory virtue (all of which can be found in Sober 1984b). He gives examples, such as Fisher's explanation of the

prevalence of 1:1 sex ratios and the population genetic account of heterosis. He draws an analogy between this style of biological theorizing and the explanations of intentional psychology. Finally, he argues that providing these kinds of explanations would be part of the scientific enterprise even if, like Laplace's demon, our knowledge at the physical level were complete. A discussion of these arguments, however, is beyond the scope of this paper.

[7]Beatty has acknowledged this, both in conversation and in Beatty (1987).

[8]An alternative is to ground their explanatory legitimacy in something other than lawhood. Philip Kitcher (1981,1985), for example, sees explanatory virtue as a matter of unification, but does not presuppose that laws of nature function as the unifying principles. In my dissertation I have also developed an account of this kind of explanatory virtue, one that, unlike Kitcher's, leaves room for causal explanation as well. Finally, there are indications that Sober himself, despite his debate with Rosenberg over the existence of source laws, is sympathetic to such an approach. In discussing the covering-law tradition he says: "...no argument was ever offered for why there must be a part of the story that is both general and empirical at once. I suggest that this requirement on explanation should be discarded." (Sober 1984b, p. 80)

References

Beatty, J. (1980). "Optimal-Design Models and the Strategy of Model Building in Evolutionary Biology." *Philosophy of Science* 47: 532-561.

_____. (1981). "What's Wrong with the Received View of Evolutionary Theory?" *PSA* 1980, Volume 2, R. Giere and P. Asquith (eds.). East Lansing: Philosophy of Science Association, pp. 397-426.

_____. (1987). "On Behalf of the Semantic View." *Biology and Philosophy* 2: 17-23.

Brandon, R. N. (1978). "Adaptation and Evolutionary Theory." *Stud. Hist. Phil. Sci.* 9: 181-206.

_____. (1981). "A Structural Description of Evolutionary Theory." *PSA* 1980, Volume 2, R. Giere and P. Asquith (eds.). East Lansing: Philosophy of Science Association, pp. 427-439.

Brandon, R. N. and Beatty, J. (1984). "The Propensity Interpretation of 'Fitness'." *Philosophy of Science* 51: 342-347.

Kitcher, P. (1981). "Explanatory Unification." *Philosophy of Science* 48: 507-531.

_____. (1985). "Darwin's Achievement." in Rescher, N. (ed.), *Reason and Rationality in Natural Science*, University Press of America, pp. 127-189.

Lloyd, E. A. (1984). "A Semantic Approach to the Structure of Population Genetics." *Philosophy of Science* 51: 242-264.

Mills, S. K. and Beatty, J. (1979). "The Propensity Interpretation of Fitness." *Philosophy of Science* 46: 263-286.

Nagel, E. (1961). *The Structure of Science.* New York: Harcourt, Brace & World.

Rosenberg, A. (1978). "The Supervenience of Biological Concepts." *Philosophy of Science* 45: 368-386.

_____. (1982). "On the Propensity Definition of Fitness." *Philosophy of Science* 49: 268-273.

_____. (1983). "Fitness." *The Journal of Philosophy* LXXX: 457-473.

_____. (1985). *The Structure of Biological Science.* New York: Cambridge.

Rosenberg, A. and Williams, M. B. (1986). "Fitness as Primitive and Propensity." *Philosophy of Science* 53: 412-418.

Sober, E. (1983). "Equilibrium Explanation." *Philosophical Studies* 43: 201-210.

_____. (1984a). "Fact, Fiction, and Fitness: A Reply to Rosenberg." *The Journal of Philosophy* LXXXI: 372-383.

_____. (1984b). *The Nature of Selection.* Cambridge, Mass.: Bradford/MIT Press.

_____. (1987). "Does Fitness Fit the Facts? A Reply to Williams and Rosenberg's Rejoinder." *The Journal of Philosophy* LXXXIV: 220-223.

Thompson, P. (1983). "The Structure of Evolutionary Theory: A Semantic Approach." *Stud. Hist. Phil. Sci.* 14: 215-229.

van Fraasen, B. C. (1980). *The Scientific Image.* Oxford: Clarendon Press.

Waters, K. C. (1986). "Natural Selection Without Survival of the Fittest." *Biology and Philosophy* 1: 207-225.

Williams, M. B. (1970). "Deducing the Consequences of Evolution: A Mathematical Model." *Journal of Theoretical Biology* 29: 343-385.

Williams, M. B. and Rosenberg, A. (1985). ""Fitness" in Fact and Fiction: A Rejoinder to Sober." *The Journal of Philosophy* LXXXII: 738-748.