Natural Selection Without Survival of the Fittest

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ABSTRACT: Susan Mills and John Beatty proposed a propensity interpretation of fitness (1979) to show that Darwinian explanations are not circular, but they did not address the critics' chief complaint that the principle of the survival of the fittest is either tautological or untestable. I show that the propensity interpretation cannot rescue the principle from the critics' charges. The critics, however, incorrectly assume that there is nothing more to Darwin's theory than the survival of the fittest. While Darwinians all scoff at this assumption, they do not agree about what role, if any, this principle plays in Darwin's theory of natural selection. I argue that the principle has no place in Darwin's theory. His theory does include the idea that some organisms are fitter than others. But greater reproductive success is simply inferred from higher fitness. There is no reason to embody this inference in the form of a special principle of the survival of the fittest.

KEY WORDS: Fitness, propensity, tautology, untestable, semantic view of theories.

1. INTRODUCTION

> My dear Darwin, I have been so repeatedly struck by the utter inability of numbers of intelligent persons to see clearly, or at all, the self-acting and necessary effects of Natural Selection, that I am led to conclude that the term itself, and your mode of illustrating it, however clear and beautiful to many of us, are yet not the best adapted to impress it on the general naturalist public.

Thus began Alfred Russell Wallace. Wallace was writing to Charles Darwin about criticisms based on the misconception that natural selection must depend on an intelligent chooser. "Now I think this arises," continued Wallace,

> almost entirely from your choice of the term Natural Selection, and so constantly comparing it in its effects to man's selection, and also to your so frequently personifying nature as 'selecting,' as 'preferring,' as 'seeking the good of the species,' etc., etc. (July 2, 1866: Marchant 1916, pp. 140–1)

To those of us living in the age of "creation science", there is irony in the fact that Wallace made the following proposal in order *to prevent* critics from basing their attacks on misrepresentations of Darwin's theory: "I wish, therefore, to suggest to you the possibility of entirely avoiding this source of misconception ... by adopting Spencer's term (which he

generally uses in preference to Natural Selection), viz. 'Survival of the Fittest'." Spencer's 'survival of the fittest', Wallace claimed, "is a compact and accurate definition of natural selection." (Marchant 1916, p. 142) Darwin apparently concurred. He responded, "I fully agree with all that you say on the advantages of H. Spencer's excellent expression of 'the survival of the fittest.' " (Marchant 1916, p. 144) Darwin adopted the phrase and even added it to the last two editions of the *Origin*.

Today, many Darwinians take a less enthusiastic view of Spencer's expression. For example, Gavin de Beer wrote, "It is regrettable that Darwin in later years allowed himself to be persuaded to accept Herbert Spencer's inappropriate expression 'survival of the fittest.' " One of the faults de Beer found with the expression is that "It lays the subject open to the taunt of tautology: Who survive? The fittest. Who are the fittest? Those who survive." De Beer, a biologist and historian of science, placed the blame not on Wallace, the naturalist who persuaded the aging Darwin to adopt the term, but on Spencer, the philosopher who coined the troublesome phrase. "It was not the first (or the last) time," complained de Beer, "that so-called philosophers of science have encumbered scientists with their help." (de Beer 1971, p. 573) I hope to atone for Spencer's transgression by straightening out the conceptual mess behind the argument that Darwin's theory is unscientific because the fittest must by definition survive.

I will show that there is more to the critics' claim that the principle of the survival of the fittest is true by definition than defenders of Darwinism have acknowledged. The problem with the critics' argument that the theory is unscientific lies not with their conclusion about the logical status of the principle of the survival of the fittest (i.e. what many writers refer to as "the principle of natural selection"), but with their understanding of the relationship between this principle and Darwin's overall theory of natural selection. I will suggest, in fact, that even the philosophers who have come to Darwin's defense do not have a clear understanding of the foundations of Darwin's original theory or the role played by the principle of the survival of the fittest. My ultimate aim is to present an account of Darwin's theory that will show just where the critics, as well as the defenders, go wrong.

My treatment of the principle of the survival of the fittest and Darwin's theory of natural selection is based upon the propensity interpretation of fitness. Although Robert Brandon (1978), and Susan Mills and John Beatty (1979) proposed this interpretation to show why certain kinds of Darwinian explanations are not circular, they did not carry out an in-depth analysis of the critics' arguments concerning the principle of the survival of the fittest. I will motivate an account of Darwin's theory by using the propensity interpretation of fitness to carry out such an analysis. I begin by reviewing the critics' arguments and examining the status of the

principle of the survival of the fittest. Next I consider Brandon's description of evolutionary theory and discuss his rationale for including a version of the principle of the survival of the fittest in the core of his reconstruction. Finally, I present an alternative formulation of the theory of natural selection to show that the principle of the survival of the fittest is not an essential component of Darwin's theory.

2. THE CRITICS' ARGUMENTS

The critics' arguments concern what many take to be the principle of natural selection, namely the survival of the fittest. But what does this catch phrase really mean? It is commonly interpreted to assert that if an organism is fittest, then it will survive. Or more correctly, if an organism is fittest, then it will probably survive. Or even better, if an organism is fitter than another of the same species in their common environment, then the individual with higher fitness will have a greater probability of surviving. 'Survival' has a special meaning in this context. Here, survival is more than just not dying; it includes leaving behind viable progeny. And fitness is not just related to living, but also concerns reproductive success. So the principle of the survival of the fittest, in its sophisticated form, means that an organism with higher fitness in (environment) E will probably have greater reproductive success in E than conspecific organisms with lower fitnesses.

A. Manser (1965), K. R. Popper (1974), J. J. C. Smart (1963), and numerous others have formulated various arguments concluding that the principle of the survival of the fittest is *tautological.* All of these arguments rest on a common allegation: fitness cannot be *defined* independently of actual survival. If the fittest can only refer to those who actually survive, then "the survival of the fittest" just says that those who survive are those who survive. This argument is often conflated with the following variation of it, which concludes that the principle is *untestable.* The untestability argument starts from the premise that fitness cannot be *determined* independently of actual survival. Thus, the argument goes, it is impossible to disprove that the fittest survive because no individual could be known to be fittest unless it was already known to have survived.

Although the critics couch their arguments in terms of a crude version of the principle of the survival of the fittest, their arguments apply to sophisticated versions as well. For example, consider the formulation, "fitter organisms will probably have greater reproductive success than less fit organisms." If the fitness of the organisms cannot be *defined* independently of actual reproductive success, then this formulation just asserts that an organism having greater reproductive success probably has greater reproductive success than organisms with lower reproductive success. And

if fitness cannot be *determined* independently of actual reproductive success, then we could never find a disconfirming instance because no organism could be identified as fitter than another unless it was already known to have greater reproductive success. Thus, the challenge for the Darwinians seems to be to show that fitness is logically independent of actual reproductive success *and* that it can be independently determined.

3. THE PROPENSITY INTERPRETATION OF FITNESS

The propensity interpretation of fitness finally makes clear what many Darwinians have long believed, but never adequately explained: fitness is logically independent of actual survival. According to Mills and Beatty, "... the fitness of an organism is its propensity to survive and reproduce in a particularly specified environment and population." (Mills and Beatty 1979, p. 270) Mills and Beatty elaborate on what they mean by propensity:

> When we say that an entity has a propensity (disposition, tendency, capability) to behave in a particular way, we mean that certain physical properties of the entity determine, or are causally relevant to, the particular behavior whenever the entity is subjected to appropriate 'triggering conditions.' (Mills and Beatty 1979, pp. 201—1)

This view renders fitness logically independent of actual reproductive success because, as we all know, the most capable do not necessarily succeed. For example, a very well-adapted organism may be killed by a bolt of lightning, but this does not mean that it was not fitter than its maladapted cousin who happened to be a few yards away when lightning struck. So fitness is not necessarily the property of those who actually reproduce. Rather, fitness is the property of those who, given the match between their traits and their environment, have (or had) the best chance of reproducing.

According to the propensity interpretation, there are two ways to determine fitness. It can be estimated from actual rates of reproductive success or inferred from an analysis of the match between the environment and the organism.[1] In fact, biologists appeal to both methods. Hence, fitness can be determined independently of actual reproductive success.

Acceptance of the propensity interpretation of fitness means that the problem concerning the status of the principle of the survival of the fittest can finally be resolved. Although not everyone accepts the propensity interpretation (for example, see Rosenberg 1982 and 1983), I will not directly defend it here. Instead, I refer readers to the persuasive arguments presented by Mills and Beatty (1979), R. Brandon (1978), E. Sober (1981), R. Burian (1983), and Brandon and Beatty (1984). My task here is to spell out the implications of this interpretation. One implication of the propensity interpretation is that the critics' arguments which conclude

that the principle is tautological and untestable rest on false premises, for fitness can be defined and determined independently of actual reproductive success. Ironically, however, the critics' conclusions concerning the logical status of the principle of the survival of the fittest are correct.

4. PROPENSITY AND "THE SURVIVAL OF THE FITTEST"

I began my analysis of the status of the principle of the survival of the fittest by offering the following formulation of the principle:

P1   Organisms with higher fitnesses in (environment) E will probably have greater reproductive success in E than (conspecific) organisms with lower fitnesses.

"E" is meant to specify the organisms' real environment which includes possibilities such as catastrophic events that indiscriminately eliminate organisms. Ideally, all potential environmental factors and their likelihood of occurrence would be included in the specification of E. In reality, of course, this cannot be carried out.

This conception of the environment differs from the one offered by Mills and Beatty in their analysis of fitness (1979). They suggest that the specification of the environment should not include factors that would "separate successful from unsuccessful reproducers without regard to physical differences between them." (Mills and Beatty 1979, p. 272) Hence, they do not view fitness as the propensity an organism actually has in its real environment; rather, they interpret it as the propensity an organism would have in a hypothetical environment (one without the possibility of capricious elements indiscriminately eliminating organisms).[2]

One problem with excluding undiscriminating factors from our specification of the environment is that it obscures one of Darwin's key insights: the net effect of all environmental factors is to eliminate organisms according to physical differences. When Darwin described the delicate balance in nature and the struggle for existence,[3] he was not just claiming that variations would give some organisms a better chance to live and reproduce in some ideal environment without capricious factors. Rather, he was trying to show that differences, including small ones, could affect an organism's chances for success in its real environment. Our specification of the environment should not disregard undiscriminating factors; it should give all factors their proper weight.

The fact that fitter organisms are occasionally eliminated by undiscriminating factors does not, of course, disconfirm the principle of the survival of the fittest. For the possibility that a fitter organism might become trapped in circumstances where its variations do not bestow any advantage does not necessarily indicate that the organism lacks a

greater chance for success in the environment *as a whole*. But what if the environment as a whole contained a preponderance of factors that eliminated organisms without regard to their variations? In this case, the principle of the survival of the fittest would not be in jeopardy because in such an environment there would be no organisms with greater propensities for reproductive success. The Darwinian tenet in trouble would be the claim that physical variations produce differential propensities for reproductive success (i.e. produce differential fitnesses).

The status of the principle of the survival of the fittest depends not just on how one chooses to interpret fitness, but also on how one decides to **interpret the "probably" in the principle (see P1 on page 211).** There are two basic kinds of objectivist interpretations of probability to choose from: the propensity and frequency interpretations. If the propensity interpretation is applied, the principle turns out to be an analytic truth[4] (i.e. true by definition). If the frequency interpretation is used, the resulting principle is synthetic (not true or false by definition) but not testable. Although simplicity seems to favor treating the "probably" in terms of propensity, I will discuss the implications of applying each interpretation.

If the "probably" in the principle of the survival of the fittest, P1, is interpreted in terms of propensity, the principle can be translated as follows:

P2   Organisms with higher fitness in E will have a greater propensity for reproductive success in E than (conspecific) organisms with lower fitness.

But since higher fitness just means a greater propensity for reproductive success, this only says that organisms with a greater propensity for reproductive success have a greater propensity for reproductive success. So, if both "probably" and "fitter" are interpreted as propensities, the principle of the survival of the fittest, as critics have long maintained, is analytically true.

The other kind of objectivist interpretation of probability, the frequency interpretation, could give the following meaning to the principle of natural selection:

P3   At any time, *t*, organisms with sufficiently higher fitnesses at *t* have greater actual reproductive success than (conspecific) organisms with lower fitnesses in a high proportion of cases.

I will call this statement the "frequency version of the principle." It is important to emphasize that I am retaining the propensity interpretation of *fitness* in this formulation (acceptance of which is a premise of this paper and argument). According to this interpretation, fitness is the propensity (or ability) of an organism to reproduce successfully in a specified environment.

The propensity interpretation of fitness does not deductively imply that the actual frequency of reproductive success must approximate the propensity for reproductive success, even in an infinite sequence of trials (see R. Giere 1973, pp. 477—8). The frequency version of the principle of the survival of the fittest connects the propensity for reproductive success (i.e. fitness) with the actual frequency of success. In effect, it is an application of the principle of induction which licenses one to conclude that actual frequencies approximate propensities.

The frequency version of the principle of the survival of the fittest is synthetic, for however unlikely, it is still possible that those with the greatest propensities for reproductive success do not actually reproduce most successfully, even over the entire (past and future) history of biological evolution (i.e. the fittest may have incredibly bad luck). Thus, a proponent of the principle of the survival of the fittest might argue that the central empirical tenet of Darwinian theory states that the actual frequencies of reproductive success approximate the propensities for such success.

Although the frequency version of the survival of the fittest is synthetic, it is in principle untestable. The frequency version of the principle may seem testable because instantiations of it can indeed be tested. For example, we could test the claim that organisms with some particular trait, such as having the ability to resist a deadly disease have greater reproductive success in a specified environment than organisms belonging to the same population that do not have this particular trait. What we cannot test is the second-order principle that organisms with greater propensities to reproduce successfully have greater reproductive success.

The frequency version of the principle cannot be tested because it concerns the continuation of bad luck. If one tries to establish a claim that something (or some group of things) will continue to be unlucky, one will run up against a casino operator's version of the gambler's fallacy. According to the gambler's fallacy, a gambler thinks that he will be extra lucky in the future because he has been so unlucky in the past. For example, he may have lost at the roulette wheel every day for an entire year despite the fact that the odds against this streak of bad luck were ten thousand to one. The casino operator, on the other hand, might reason that since the gambler was so unlucky in the past, he will always be unlucky. As all students of probability theory know, both are wrong. Such deviations from what is likely cannot be inferred. The casino operator might infer that the wheel is not fair and thus that the gambler is not unlucky in the true sense of the term. In this case, the operator could reasonably conclude that the gambler will continue to lose. But if the operator insists that the wheel is fair and that the gambler is truly unlucky, then he cannot infer that the gambler will continue to be truly unlucky in the future.

Biologists trying to disconfirm the frequency version of the principle of the survival of the fittest, P3, would be in essentially the same position as

the casino operator. We might imagine a team of biologists trying to disconfirm the principle. They begin by performing an ecological-phy-siological-etc. analysis to determine the fitnesses of various conspecific organisms in some environment. Afterwards, they observe the actual frequency of reproductive success. Now suppose the biologists discover that the organisms which they had initially concluded must have greater propensities for reproductive success actually had significantly less success than the others. What would they conclude? They would probably con-clude that important factors have been overlooked in their original analysis. That is, they would conclude that the organisms which they had initially thought had greater propensities for reproductive success in fact did not.

One might object that although the above illustration suggests that the principle is not testable in practice, it does not show that the principle is untestable in principle. In principle, this objection would go, the biologists could carry out such an in-depth analysis of the organisms and their environment that the results of their study would practically be guaran-teed. The biologists would be completely justified in believing that they had determined (correctly) the organisms' propensities for reproductive success (i.e. their fitnesses). In principle, the biologists could also examine a number of large samples and calculate the frequency of reproductive success for the various organisms. Now suppose they regularly found that the organisms, which they had determined to have greater propensities for reproductive success, did not have higher actual rates of success. Wouldn't this provide good evidence against the frequency version of the principle? The answer is no. Even if this fantastic situation obtained, we would not have evidence against the claim that in the future the actual frequencies of reproductive success would not approximate the real propensities for such success. We might have excellent reason to conclude that this was not the case in the observed samples, but like the casino operator, we cannot infer that those who were *truly* unlucky in the past will be *truly* unlucky in the future. If we insist, as the casino operator might, that we *know* the relevant propensities, then we can only conclude that we have witnessed an excep-tionally improbable sequence of events which will very probably not be repeated in the future.

The relation between the gambler's fallacy and the untestability of the frequency version of the principle can be made explicit by connecting the notions of probability and propensity. According to some philosophers, physical propensities offer the only viable interpretation of probability (for example, see Giere 1973 and 1976). For our purposes, we need assume only that the physical dispositions which we call propensities model the theorems of probability. Assuming that propensities do model probability, we can reformulate the gambler's fallacy as follows. Suppose that a penny has a propensity of 0.5 to land on heads. Then just because it landed on

tails 10 times in a row does not mean it now has a greater (or lesser) chance to land on heads. For there is no causal interaction between the *outcome* of the earlier trials and the distribution of later trials. Notice that we are assuming that there is no connection between the "luck" of one trial and the "luck" of later trials. If the propensity of the coin landing on heads is really 0.5, then the distribution of later outcomes depends on that propensity and not on the distribution of earlier outcomes. The same is true of organisms. The reproductive success of organisms depends on their propensities for reproductive success (i.e. their fitnesses), not on whether previous organisms with higher fitnesses actually had greater reproductive success. The only connection between the outcomes of future and past distributions, as in the case of the penny, is provided by the underlying propensities. Thus, any inference about future distributions based on past ones must assume that the frequencies have and will approximate propensities. But this is just what we would be calling into question if we tried to disconfirm the frequency version of the principle of the survival of the fittest.

I wish to stress that I am not claiming that all statistical generalizations are untestable. I am only arguing that a special class of them involving the continuation of back luck cannot be tested. The statistical version of the principle of the survival of the fittest involves bad luck because it states that in a large number of cases, fitter organisms will not be unlucky (i.e. their actual rate of success will measure up to their propensities for such success). In contrast to the frequency version of the principle, most statistical generalizations do not concern deviations from propensities and thus can be tested in the usual manner. One can test such generalizations by observing the frequency of the target property in an appropriately selected sample. For example, one could test instantiations of the principle of the survival of the fittest such as the claim that organisms with some particular trait have greater reproductive success than conspecific organisms lacking that trait in a specified environment. To test such a claim, one could observe the relative frequencies of reproductive success of organisms with and without the trait in appropriately selected samples. One could then, at some particular confidence level, make inferences about the relative frequencies of reproductive success in unobserved populations. Although there is no way to completely eliminate the possibility of a sampling error (even if the procedure is carried out correctly), the possibility of error can be decreased by examining larger samples.[5]

In summary, unlike the case of testing one of its instantiations, testing the frequency version of the survival of the fittest presupposes that we fully understand the underlying causal factors and already know the propensities for the target property (reproductive success). Suppose we observe sample frequencies that do not match the propensities. Given the complexity of the underlying biological system, the most reasonable

conclusion in the real situation would be that important causal factors must have been overlooked and that the frequencies do indeed approximate the true propensities (but *not* our estimates of the propensities). If, however, biologists were extremely confident in their analysis of the underlying causal situation, then they might reasonably conclude that the chance of sampling error was greater than the chance of miscalculating the relevant propensities. In fact, under certain conditions the chance of sampling errors could be significant (see Note 5). One cannot, however, reasonably conclude both that they correctly calculated the underlying propensities and that there were no sampling errors.

The critics were correct about the status of the principle of the survival of the fittest; it is either analytically true (under the propensity interpretation of probability) or untestable (under a frequency interpretation of probability). But this does not necessarily imply that something is wrong with Darwinian theory. For the critics have not established that the fate of Darwinian theory is linked to the status of the principle of the survival of the fittest. One way to break the link would be simply to dispense with the principle which, at best, links propensities with actual frequencies. After all, analogous principles are not included in the specification of other theories. For example, consider the theory of solubility. Mills and Beatty suggest that the fitness of an organism explains its success in much the same way that the solubility of a substance explains its dissolution: by relating its behavior to physical properties that are causally relevant. Chemists, however, do not appeal to a special "principle of the dissolution of solubles." Rather, they simply infer that soluble substances actually dissolve under the appropriate conditions. Why shouldn't biologists, in a similar way, infer that fitter organisms are actually more successful? Does the principle of the survival of the fittest play any role other than that which could be played by the principles of inference that are used in other sciences?

5. BRANDON'S ACCOUNT OF EVOLUTIONARY THEORY

According to Robert Brandon, the principle of the survival of the fittest — or as he calls it, the principle of natural selection — does indeed have an additional and vital role in evolutionary theory. Brandon has presented a sophisticated account of evolutionary theory making use of recent philosophical insights such as the propensity interpretation of fitness (Brandon 1981). Furthermore, he provides what at least seems to be good reason for accepting his claim that the principle of the survival of the fittest is the "cornerstone of Darwinian theory." (Brandon, 1981, p. 428)

On Brandon's account of evolutionary theory, the principle of the survival of the fittest (which he, as many others, calls the "principle of

natural selection") provides the basis of Darwinian explanations of differ-
ential reproductive success. While he argues that the principle is untest-
able (Brandon, 1978, p. 202) and has no empirical biological content
(Brandon 1981, p. 432), he calls it the "most important part of evolu-
tionary theory." (Brandon 1981, p. 438) In anticipation of the critics,
Brandon writes:

> It does not follow from this [that the principle has no empirical biological content] that
> the critics of the principle of natural selection have been right. They, taking a simple-
> minded view of the structure of scientific theories, have assumed that a principle with
> no empirical biological content cannot play a prominent role in a biological theory.
> (Brandon 1981, p. 432)

I wish to make it clear that I am not necessarily assuming that a principle
must have biological content to be a part of a biological theory. Rather, I
am trying to determine what role, if any, the principle of the survival of the
fittest plays in the theory of natural selection. Given my analysis, one
might think that the principle plays the role of an inductive inference rule
that connects propensities with actual frequencies. But then it is not clear
why one should formulate a special principle of induction for this partic-
ular theory. That is, why shouldn't biologists reason as other scientist do
and simply infer actual events from the propensities for such events?

Before I describe Brandon's account of evolutionary theory, a termino-
logical matter needs to be discussed. Brandon independently offered a
proposal essentially equivalent to the Mills-Beatty propensity interpreta-
tion of fitness. But what Mills and Beatty call "fitness" (i.e. propensity for
reproductive success), Brandon calls "adaptedness". Brandon thinks it is
best to reserve the term "fitness" for actual reproductive success because
population biologists often use it that way. This is a purely verbal disagree-
ment and I will not try to settle it here. Since it would confuse the issue to
use both sets of terminology, however, I have taken the liberty of describ-
ing Brandon's views in Mills and Beatty's terms, rather than in his own.
Hence, I will continue to use "fitness" to denote the propensity for
reproductive success and not actual reproductive success.

According to Brandon's description, evolutionary theory contains a
core, a "slightly less central" principle, and peripheral instantiations. The
core is made up of the principle of the survival of the fittest and the
following two biological tenets:

T1   Biological entities are chance set-ups with respect to reproduc-
       tion. (Brandon 1981, p. 437)

T2   Some biological entities differ in their ... [fitness] ... to their
       common environment, this difference having its basis in differ-
       ences in some traits of the entities. (Brandon 1980, p. 437)

The first of these tenets means that individual organisms can have, within a range of possibilities, any number of viable progeny just as individual spins of the roulette wheel may point to any of several numbers (see Brandon 1980, p. 434). The second core tenet (T2) seems to presuppose the first because it implies that the chances for reproductive success posited by the first tenet vary according to differences in traits. In any case, Brandon is correct when he writes that both of these tenets must hold if the principle of the survival of the fittest applies to a given situation. For the survival of the fittest cannot apply to a situation unless some organisms are more fit than others.

Brandon calls the following principle "slightly less central" because it is not, as he puts it, a "presupposition of the applicability" of the principle of the survival of the fittest:

T3   [Fitness] is to a degree heritable, or equivalently, the causal basis of ... [fitness] ... values are to a degree heritable. (Brandon 1980, p. 437)

The special role which Brandon attributes to the principle of the survival of the fittest concerns instantiations of the principle. He formulates the principle as follows:

P4   (Probably) If a ... [has higher fitness] ... than b in E, then a will have more offspring than b. (Brandon 1980, p. 432)

Brandon notes that even though this principle has no empirical biological content, instantiations of it do. "In such instantiations," he writes, "the dispositional relation of ... [fitness] ... is cashed out in terms of differences in particular traits." (Brandon 1980, p. 432) He provides the following example of an instantiation:

I1   (Probably) If moth a has darker colored wings than moth b, then a will have more offspring than b in E. (Brandon 1980, p. 433)

As Brandon sees it, the principle of the survival of the fittest serves "to structure particular biological explanations of differential reproduction." (Brandon 1980, p. 432) In the case of this instantiation, wing color is employed to explain differential reproductive success. As Brandon states, and as I have explained in section 4, instantiations such as I1 are testable (even though the principle itself is not).

Brandon argues that the principle of the survival of the fittest is crucial because without it there could be no general statement of the theory.[6] He views instantiations such as I1 as low-level theories about the evolution of a certain population in its environment. Without the principle of the survival of the fittest, he argues, there would only be "numerous uncon-

nected low-level theories concerning the evolution of particular popula-
tions in particular environmental settings." (Brandon 1980, p. 433)

The difficulty of giving a general statement of evolutionary theory
seems to stem from the fact that biologists have been hard-pressed to
formulate any universal laws of evolution. According to some traditional
views, scientific theories all contain such laws and one can give a general
statement of a theory simply by specifying its laws (and the appropriate
connecting principles). But as Brandon points out, the second core tenet is
not universal (Brandon 1980, p. 435). And according to Beatty, there are
no universal laws of evolutionary theory (see Beatty 1980). Assuming then
that there are no universal laws in Darwinian theory, the question is: What
connects Darwinian descriptions of particular evolutionary processes?
According to Brandon, the principle of the survival of the fittest provides
the link. Beatty (1980) offers a different proposal. He suggests, in line with
the proponents of the semantic view of theories, that the theory provides a
definition of a kind of system. Accordingly, Darwinian descriptions of
various evolving populations are united by the fact that they all fit the
same general structure defined by Darwinian theory. So whereas Brandon
suggests that only the principle of the survival of the fittest can provide the
general structure that unites Darwinian descriptions, the view advanced by
Beatty, and more recently by E. Lloyd (1984) and P. Thompson (1983),
suggests that the general structure is defined by the theory as a whole. I
will show that if we adopt the latter view, we can formulate a general
statement of Darwin's original theory of natural selection without the
principle of the survival of the fittest.

6. DARWIN'S THEORY OF NATURAL SELECTION

The proponents of the semantic view offer an important insight for
clarifying Darwin's theory of natural selection. Whereas traditional views
of scientific theories suggest that theories are presented in the form of
general theorems, advocates of the semantic view stress that theories are
often presented by identifying a family of physical, or in this case
biological, systems that model the theory (for example, see P. Suppes
1967 and van Fraassen 1980, pp. 42, 64).[7] This is particularly important
in the case of formulating Darwin's theory of natural selection because he
never explicitly separated the presentation of his theory from his justifica-
tion of it. The danger with trying to formulate his theory on the basis of
the generalizations in the *Origin* is that one might easily confuse general-
izations that Darwin offered only to justify his theory with the theory itself.
A better approach to specifying his theory is to examine the models (i.e.
examples) of natural selection presented by Darwin and try to identify the

kind of system that they exemplify. Darwin, in fact, offered paradigmatic models of natural selection in the form of "imaginary illustrations."

The task of specifying Darwin's theory is confounded not just by the fact that he presented and argued for it simultaneously, but also because he never clearly separated his theory of natural selection from his other evolutionary views. Darwin was not only arguing for the theory of natural selection, but he was also trying to establish the fact of evolution itself and the different causal mechanisms by which it proceeded. His overall theory of evolution included mechanisms which are now often referred to as "non-Darwinian", such as the inheritance of acquired characteristics. One of Darwin's aims in presenting these different causal mechanisms was to show that evolution could be accounted for entirely by means of natural causes. I will not try to clarify these so-called non-Darwinian mechanisms or the implicit claim that collectively they provided a naturalistic explanation of evolutionary change. Instead, I will focus only on what Darwin called natural selection. In addition, it is not my intention to distinguish the many versions of natural selection that Darwin described. Rather, I hope to clarify the general idea that underlies all of them.

One of Darwin's imaginary illustrations of natural selection concerned the co-adaptation of a nectar producing plant species and a species of bees. After discussing how the flowers might become adapted to the bees which disperse their pollen, Darwin briefly discussed the adaptation of the bees:

> I could give many facts, showing how anxious bees are to save time; for instance, their habit of cutting holes and sucking the nectar at the bases of certain flowers, which they can, with a very little more trouble, enter by the mouth. Bearing such facts in mind, I can see no reason to doubt that an accidental deviation in the size and form of the body, or in the curvature and length of the proboscis, &c., far too slight to be appreciated by us, might profit a bee or other insect, so that an individual so characterized would be able to obtain its food more quickly, and so have a better chance of living and leaving descendants. Its descendants would probably inherit a tendency to a similar slight deviation of structure. (Darwin 1959, p. 94)

In this illustration, as well as in all his others, Darwin alludes to three factors: variation, chances to live and leave descendants, and inheritance. He concluded his illustration by explaining that natural selection works by accumulating small variations:

> Thus I can understand how a flower and a bee might slowly become, either simultaneously or one after the other, modified and adapted in the most perfect manner to each other, by the continuous preservation of individuals presenting mutual and slightly favorable deviations of structure. (Darwin 1959, p. 95)

An examination of such illustrations show that Darwin's models of natural selection embody the following three conditions:

i. Variation of traits within a species is accidentally produced without regard to adaptative advantage.[8]

ii. Accidentally produced variations cause differential fitness (i.e. differential chances, or propensities, for descendant contribution) in the individuals of a species in their environment.

iii. Accidentally reproduced variations are inherited through a mechanism which is consistent with the accumulation of variations over successive generations resulting in changes of evolutionary magnitude.

My claim is that these three conditions identify the kind of biological system that Darwin intended to specify with his theory of natural selection. In other words, these are the general conditions that a biological system must satisfy in order to be covered by the theory of natural selection.

One might object that conditions i—iii are not sufficient because they do not specify that the system is necessarily evolving; they only imply that it is very probable that the species would evolve. That is, a system might satisfy these conditions and not evolve because the individuals with the greatest chance to reproduce successfully are unlucky and are no more successful than their competitors. According to this objection, conditions i—iii need to be supplemented with the condition that the actual frequency of reproductive success approximates the propensities for such success (i.e. the frequency version of the principle of the survival of the fittest, P3) because only then would the theory necessarily specify only evolving systems.

The problem with this objection is that it seems to confuse theory with explanation. A theory describes the structure of the world which makes particular events possible, probable, or perhaps even necessary. Explanations, on the other hand, deal directly with historical events and identify the relevant causal factors. Biologists try to explain the course that evolution has taken (a historical event) with various evolutionary theories, but that does not mean that the explanations are necessarily components of the theories. The theory of natural selection identifies a structure exemplified by biological systems which made the outcome of evolution highly probable.[9]

The theory of natural selection can be used to explain a particular evolutionary history. The Hempelian version of this explanation would apply the principle of induction that allows one to infer actual frequencies from propensities (in this case the frequency of reproductive success from the propensity for such success). As I have explained, the frequency version of the principle of the survival of the fittest, P3, is an application of this inductive principle. Therefore, one could view the frequency version of the principle as the inference rule that connects the explanans with the explanandum in Darwinian explanations. Thus, the frequency

version of the principle can be interpreted as playing an important role in Darwinian *explanations* without being a component of the general *theory*.

In another sense, this account of Darwin's theory of natural selection is incomplete for the extent to which these conditions apply is left unspecified. For example, should one say that the first condition is satisfied if only a few traits, among innumerable ones, were associated with accidentally produced variations? Moreover, to what extent do the conditions of Darwin's theory need apply in order for the theory to be acceptable or important? It is difficult to find clear answers to these questions in Darwin's writings. He seems to have argued that these conditions are satisfied throughout nature, but perhaps he did so only as a means to establish that natural selection was prominent enough to account for adaptation.

The fact that this approach to formulating Darwin's theory does not require one to specify the scope of its conditions is a virtue, not a vice. For the significance of Darwin's theory did not stem from the belief that natural selection was everywhere occurring, but from the idea that natural selection could explain the adaptation that appeared everywhere. Although Darwin, and many modern-day Darwinians, might think that natural selection is a ubiquitous phenomenon, the significance of the theory does not depend on such a broad claim. If natural selection accounts for adaptation, then it is an important theory regardless of whether it is always occurring. On the other hand, if the theory does not truly account for adaptation, then it is much less important than Darwin and his followers believed. The importance of the theory of natural selection, then, depends not upon the generality of its central tenets, but upon the extent to which it can be applied to explain the phenomena of adaptation.

7. CONCLUSION

The critics of natural selection claim that the theory is unscientific because the principle of the survival of the fittest is true by definition. One might think the account offered here only reinforces their attack because it treats Darwin's theory as a definition of a kind of biological system, rather than as a set of empirically testable laws. The reason this account does not support the critics' attack is that theoretical claims such as the claim that a particular system is Darwinian (i.e. fits the structure defined by conditions i—iii) are empirical and testable.

Such theoretical claims are vague, but only because I have formulated conditions i—iii to cover the many different types of systems that Darwin thought illustrated natural selection. In fact, Darwin's theory of natural selection would be better viewed in terms of a set of more specific definitions. Each definition would be based on the general definition

offered here, but would define a special kind of Darwinian system. For example, one definition might specify that the variations upon which selection acts are the everyday continuous type. Another might specify that the relevant variations are discontinuous. Darwin did not present a single uniform theory of natural selection and this approach would allow us to reconcile our attempt to develop an account of his natural selection theory with his actual writings.

The critics are correct about the status of the principle of the survival of the fittest; it is not a testable empirical generalization. But the critics, as well as many Darwinians, go wrong in assuming that the principle is a fundamental tenet underlying Darwin's theory. The real basis of Darwin's theory is a definition or conception of a kind of system that has a propensity to evolve because some organisms have a greater propensity to reproduce successfully than others. Differential reproductive success and the resulting evolutionary changes are simply inferred from the propensities for such. What Darwin called the "principle of natural selection" **should be construed as the existence, not the survival, of the fittest.**

NOTES

[1] A sophisticated analysis of the concept of propensity can be found in Giere (1973). Pages 477—9 are especially relevant to this point. Also see Giere (1976).
[2] John Beatty helped me clarify the point of our disagreement. He now seems to agree with what I say here about the concept of the environment. See Beatty (1984).
[3] Darwin devoted the third chapter of the *Origin of Species* to the "struggle for existence". Here, he examined the "checks" on the "natural tendency of each species to increase in number." In the next chapter he claimed that even slight variations could give an organism a better chance to live and reproduce in its environment. Although Michael Ruse once suggested that there was no significance to Darwin's characterization of the struggle for existence (Ruse 1971, pp. 343—5), I think the relevance is clear. Darwin was describing the nature of the struggle to show that slight variations could give an organism a significant advantage in overcoming the checks on its success.
[4] Roughly speaking, an analytic sentence is one that is true or false not because of some external state of affairs but solely in virtue of the meaning of its terms. An analytic sentence is either (1) a self-contradictory sentence or (2) the denial of a self-contradictory sentence. So to call a sentence analytically false is to say that it is self-contradictory. To call a sentence analytically true is to say that it denies a self-contradiction. Tautologies are analytically true sentences of a special kind (their truth can be established simply by examining their logical form). A synthetic sentence is one which is not self-contradictory *and* whose denial is not self-contradictory.
[5] Many modern evolutionists, of course, believe that certain population structures can result in making the natural counterpart to sampling errors an important element in evolution. In particular, small isolated populations are thought to accentuate genetic drift. See Beatty (1984).
[6] As Brandon points out (1980), there is an important difference between the propensity

of an organism to reproduce successfully and the propensity of a substance to dissolve. For fitness is a probabilistic disposition while solubility is a deterministic one. Nevertheless, in both cases we *infer* that a dispositional property is being manifested when the appropriate triggering conditions obtain. The difference is that in the case of reproductive success the inference is inductive, whereas in the case of dissolution, the inference is deductive.

[7] Van Fraassen holds that the presentation of a theory also includes specifying what parts of the models are intended to be direct representations of "observable" phenomena. I do not find this part of his proposal helpful in clarifying Darwin's theory.

[8] Philip Kitcher helped me clarify this condition.

[9] This distinguishes my account of the structure of Darwinian theory from those presented by Mary Williams (1970) and Richard Lewontin (1970). William's ingenious axiomization provides a good mapping of the historical course of evolution through natural selection, but it does not capture the theory of the causal factors behind that history. Lewontin's summary seems to involve related shortcomings.

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