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THE PROPENSITY INTERPRETATION OF FITNESS*

SUSAN K. MILLS AND JOHN H. BEATTY†

Indiana University

The concept of “fitness” is a notion of central importance to evolutionary theory. Yet the interpretation of this concept and its role in explanations of evolutionary phenomena have remained obscure. We provide a *propensity* interpretation of fitness, which we argue captures the intended reference of this term as it is used by evolutionary theorists. Using the propensity interpretation of fitness, we provide a Hempelian reconstruction of explanations of evolutionary phenomena, and we show why charges of circularity which have been levelled against explanations in evolutionary theory are mistaken. Finally, we provide a definition of natural selection which follows from the propensity interpretation of fitness, and which handles all the types of selection discussed by biologists, thus improving on extant definitions.

1. Introduction. The testability and logical status of evolutionary theory have been brought into question by numerous authors in recent years (e.g., Manser 1965, Smart 1963, Popper 1974). Many of the claims that evolutionary theory is not testable, that it parades tautologies in the guise of empirical claims, and that its explanations are circular, resulted from misunderstandings which have since been rebuked (e.g., by Ruse 1969, 1973 and Williams 1970, 1973a, 1973b). Yet despite the skilled rejoinders which have been given to most of these charges, the controversy continues to flourish, and has even found its way beyond philosophical and biological circles and into the pages of *Harpers Magazine*. In the spring of 1976, journalist Tom Bethell reported to the unsuspecting public that:

Darwin’s theory . . . is on the verge of collapse. In his famous book, *On the Origin of Species* . . . Darwin made a mistake sufficiently serious to undermine his theory. The machinery of evolution that he supposedly discovered has been challenged, and it is beginning to look as though what he really discovered was

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†We wish to thank Professor Michael Ruse, for initially drawing our attention to the problems of the logical status of evolutionary theory, and for insightful criticisms of an early draft of this paper. We are heavily indebted to Alberto Coffa, for providing us with explications both of propensities and of the nature of explanation, and for innumerable criticisms and suggestions. Ron Giere also suggested that the propensity interpretation was a little more complex than we originally suspected. However, we claim complete originality for our mistakes.

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nothing more than the Victorian propensity to believe in progress (1976, p. 72).

Those familiar with the details of evolutionary theory, and with the history of this controversy, will rightfully feel no sympathy with such challenges, and may wonder whether it is worth bothering with them. But the fact is that there is a major problem in the foundations of evolutionary theory which remains unsolved, and which continues to give life to the debate. The definition of fitness remains in dispute, and the role of appeals to fitness in biologist's explanations is a mystery. This is a problem which ought to concern biologists and philosophers of science, quite independent of the vicissitudes of the controversy which it perpetuates.

Biologists agree on how to *measure* fitness, and they routinely appeal to fitness in their explanations, attributing the relative predominance of certain traits to the relative fitness of those traits. However, these explanations can and have been criticised on the grounds that, given the definitions of fitness offered by most biologists, these explanations are no more than re-descriptions of the phenomena to be explained (e.g., Popper, 1974, Manser 1965, Smart 1963). Philosophers have proposed new treatments of fitness designed to avoid these charges of explanatory circularity (e.g. Hull 1974 and Williams 1973). Unfortunately, none of these interpretations succeeds in avoiding the charges, while providing a definition *useful* to evolutionary theory.

Thus it is high time that an analysis of fitness is provided which reveals the empirical content implicit in evolutionary biologist's explanations. To this end, we propose and defend the *propensity interpretation* of fitness. We argue that the propensity interpretation captures the intended reference of "fitness" as biologists use the term. Further, using this interpretation, we show how references to fitness play a crucial role in explanations in evolutionary theory, and we provide a Hempelian reconstruction of such explanations which reveals the precise nature of this role. We answer the charges of explanatory circularity levelled against evolutionary theory by showing how these charges arise from mistaken interpretations of fitness.

The concepts of fitness and natural selection are closely linked, since it is through the process of natural selection that the fittest gain predominance, according to the theory of evolution. Thus it is not surprising to find misinterpretations of fitness paralleled by misunderstandings of natural selection. The propensity analysis suggests a definition of "selection" which (unlike previously proposed definitions) accords with all the diverse types of selection dealt with by biologists.

But before proceeding with the positive analyses just promised, we consider the charge of explanatory circularity which arises from the lack of a satisfactory interpretation of fitness, and the reasons for the inadequacy of the replies so far offered in answer to the charge.

2. The Charge of Circularity. According to the most frequently cited definitions of "fitness," that term refers to the *actual* number of offspring left by an individual or type relative to the actual contribution of some reference individual or type. For instance, Waddington (1968, p. 19) suggests that the fittest individuals are those which are "most effective in leaving gametes to the next generation." According to Lerner (1958), "the individuals who have more offspring are fitter in the Darwinian sense." Grant (1977, p. 66) construes fitness as "a measure of reproductive success." And Crow and Kimura (1970, p. 5) regard fitness "as a measure of both survival and reproduction . . ." (see also Dobzhansky 1970, p. 101–102; Wilson 1975, p. 585; Mettler and Gregg 1969, p. 93).

These definitions of "fitness" in terms of actual survival and reproductive success are straightforward and initially intuitively satisfying. However, such definitions lead to justifiable charges that certain explanations invoking fitness differences are circular. The explanations in question are those which point to fitness differences between alternate types in a population in order to account for 1) differences in the average offspring contributions of those phenotypes, and 2) changes in the proportions of the types over time (i.e., evolutionary changes). Where fitness is defined in terms of survival and reproductive success, to say that type *A* is fitter than type *B* is just to say that type *A* is leaving a higher average number of offspring than type *B*. Clearly, we cannot say that the difference in fitness of *A* and *B* *explains* the difference in actual average offspring contribution of *A* and *B*, when fitness is defined in terms of actual reproductive success. Yet, evolutionary biologists seem to think that type frequency changes (i.e., evolutionary changes) can be *explained* by invoking the relative fitnesses of the types concerned. For instance, Kettlewell (1955 and 1956) hypothesized that fitness differences were the cause of frequency changes of dark and light colored pepper moths in industrial areas of England. And he devised experiments to determine whether the frequency changes were correlated with fitness differences. Several philosophers have pointed to the apparent circularity involved in these explanations. Manser (1965) describes Kettlewell's account of the frequency differences in terms of fitness differences as

. . . only a description in slightly theory-laden terms which gives the illusion of an explanation in the full scientific sense.” (1965, p. 27)

The whole idea of setting up empirical investigations to determine whether fitness differences are correlated with actual descendant contribution differences seems absurd, given the above definitions of “fitness.” If this type of charge is coupled with the assumption that the only testable claims of evolutionary theory are of this variety, (i.e., tests of whether individuals identified as “the fittest” are most reproductively successful), then it appears that evolutionary theory is not testable. As Bethell puts it,

If only there were some way of identifying the fittest beforehand, without always having to wait and see which ones survive, Darwin’s theory would be testable rather than tautological.” (1976, p. 75)

However, as Ruse (1969) and Williams (1973) have made clear, this latter charge is mistaken. Evolutionary theory embodies many testable claims. To take but one of many examples cited by Williams, Darwinian evolutionary theory predicted the existence of *transitional forms* intermediate between ancestral and descendant species. The saltationist (creationist) view of the origin of species which was accepted at the time when Darwin wrote on *The Origin of Species* predicted no such plethora of intermediate forms. Ruse has called attention to the predictions concerning distributions of types in populations which can be made on the basis of the Hardy-Weinberg law (1973, p. 36).

While these replies are well taken, they fail to clarify the role of fitness ascriptions in evolutionary theory. We agree with Williams and Ruse that evolutionary theory does make testable claims, and that many of these claims can be seen to be testable without providing an analysis of the role of fitness ascriptions. Nevertheless, some claims of evolutionary theory cannot be shown to be empirical without clarifying the role of “fitness.” Moreover, our understanding of other straightforwardly empirical claims of evolutionary theory will be enhanced by an explication of the role of “fitness” in these claims.

3. What Fitness is Not. There are two questions to be clarified in defining fitness: What sorts of entities does this predicate apply to, and what does it predicate of these entities? Both these questions have received disparate answers from various biologists and philosophers. Fitness has been claimed to apply to types (e.g., Dobzhansky

1970, pp. 101–102; Crow and Kumura 1970) as well as individuals (Lerner 1958, Waddington 1968, p. 19). As will become apparent in the course of the positive analysis, the question of what sorts of entities “fitness” applies to should not be given a univocal answer. Fitness may be predicated of individual organisms, and (in a somewhat different sense) of phenotypes and genotypes. In this section we will only consider the question of what one is predicating of individuals and types in ascribing them a fitness value, according to the various proposals under scrutiny.

Before moving on to alternatives to the definition of “fitness” in terms of actual survival and reproductive success, we need to consider the acceptability of this definition, independent of the criticism that it leads to explanatory circularity. This criticism alone is obviously not sufficient to show that the interpretation is incorrect. For, proponents of this definition can reply that fitness is actual reproductive success, since that is the way biologists use the term, and there is no other feasible definition. The fact that references to fitness lead to explanatory circularity just shows that fitness has no explanatory role to play in evolutionary theory. In fact, Bethell (1976, p. 75) makes this latter claim, and even maintains that biologists have abandoned references to fitness in their accounts of evolutionary phenomena. This is a scandalous claim.¹ A survey of evolutionary journals like *American Naturalist* and *Evolution* reveals that fitness ascriptions still play a major role in explanations of evolutionary phenomena. Indeed, the current literature on evolutionary theory reveals that the notion of fitness is of tremendous concern. Rather than abandoning the notion, modern evolutionary biologists have chosen to refine and extend it. Levins (1968) has raised the problem of fitness in changing environments. Thoday (1953) has pointed to the distinction between short term and long term fitness. An analysis, and evidence of, “variable fitness” or “frequency dependent fitness” was given by Kojima (1971). The effects of “overdominance with regard to fitness” on the maintenance of polymorphisms continues to be studied. And one very promising model of sociobiological evolution has been developed via an extension of traditional notions of fitness (the new notion is one of “inclusive fitness” (Cf. Hamilton 1964). As we will argue below, biologists are well advised *not* to abandon references to fitness, for such references play a crucial role in explanations of evolutionary phenomena.

¹ Bethell may have been misled by the fact that evolutionary biologists recognize mechanisms of evolutionary change other than fitness differences (e.g., drift). Nevertheless, there is no question that fitness differences have been and still are considered effective in producing evolutionary changes.

Fortunately, we do have grounds quite independent of the issue of explanatory circularity for deeming inadequate definitions of "fitness" in terms of actual survival and reproductive success. For, such definitions conflict with biologist's usage of the term, as is demonstrated by the following considerations. Surely two organisms which are genetically and phenotypically identical, and which inhabit the same environment, should be given the same fitness value. Yet where fitness is defined in terms of actual number of offspring left, two such organisms may receive radically different fitness values, if it happens that one of them succeeds in reproducing while the other does not. Scriven (1959) invites us to imagine a case in which two identical twins are standing together in the forest. As it happens, one of them is struck by lightning, and the other is spared. The latter goes on to reproduce while the former leaves no offspring. Surely in this case there is no difference between the two organisms which accounts for their difference in reproductive success. Yet, on the traditional definition of "fitness," the lucky twin is *far* fitter. Most undesirably, such a definition commits us to calling the intuitively less fit of two organisms the fitter, if it happens that this organism leaves the greater number of offspring of the two.²

Nor can these counterintuitive results be avoided by shifting the reference of fitness from individual organisms to groups. For, precisely as was the case with individuals, the intuitively less fit subgroup of a population may by chance come to predominate. For example, an earthquake or forest fire may destroy individuals irrespective of any traits they possess. In such a case, we do not wish to be committed to attributing the highest fitness values to whichever subgroup is left.

Since an organism's traits are obviously important in determining its fitness, it is tempting to suggest that fitness be defined entirely independently of survival and reproduction, as some function of traits. Hull (1974) hints at the desirability of such a definition. This suggestion derives *prima facie* support from the fact that given such a definition, explanations of differential offspring contribution which appeal to differences in fitness are noncircular. However, no one has seriously proposed such a definition, and it is easy to see why. The features

²The counter-intuitiveness of the traditional definition is also suggested by the following hypothetical case. Imagine two butterflies of the same species, which are phenotypically identical except that one (*C*) has color markings which camouflage it from its species' chief predator, while the second (*N*) does not have such markings and is hence more conspicuous. If *N* nevertheless happens to leave more offspring than *C*, we are committed on the definition of fitness under consideration to conclude that (1) both butterflies had the same degree of fitness before reaching maturity (i.e., zero fitness) and (2) in the end, *N* is fitter, since it left more offspring than *C*.

of organisms which contribute to their survival and reproductive success are endlessly varied and context dependent. What do the fittest germ, the fittest geranium, and the fittest chimpanzee have in common? It cannot be any concretely characterized physical property, given that one and the same physical trait can be helpful in one environment and harmful in another. This is not to say that it is impossible that some as yet unsuspected (no doubt abstractly characterized) feature of organisms may be found which correlates with reproductive success. Rather, it is just to say that we need not, and should not, wait for the discovery of such a feature in order to give the definition of "fitness."

So far, we have seen that we cannot define fitness simply in terms of survival and reproductive success. But we cannot define fitness entirely independently of any reference to survival and reproduction, either. An ingenious alternative to either of these approaches has been offered by Williams (1970, 1973). She suggests that we regard "fitness" as a primitive term of evolutionary theory, and that we therefore refuse to define it. As she points out, in the formal axiomatization of a theory, it is not possible that all terms be explicitly defined, on pain of circularity. However, the fact that we cannot formally define all the terms of a theory *within* the framework of the theory, does not prevent us from stepping outside the theory and explaining the meaning of the term in a broader linguistic framework.³ Such an explication need not amount to anything as restrictive as an operational definition or an explicit definition making the term eliminable without loss from the theory. Rather, such an explication should allow us to understand what sort of property fitness is, its relation to natural selection, and the role of references to fitness in evolutionary theorists' explanations. Thus, our criticism of Williams is not that she is wrong about fitness, but that she does not go far enough. We believe that a more thorough explication is possible, through the *propensity* interpretation of fitness.⁴

4. Propensity Analysis of Fitness. Levins (1958) has remarked that, "Fitness enters population biology as a vague heuristic notion, rich in metaphor but poor in precision." No doubt this is accurate as a characterization of the unclarity surrounding the role of fitness in evolutionary theory, even among biologists who use the term. But such unclarity is quite compatible with the fact that fitness plays

³Gary Hardegree suggested this to us in conversation.

⁴As we recently learned, Mary Williams supports the propensity interpretation and has, independently, worked toward an application of this interpretation.

an essential explanatory role in evolutionary theory. It is to the task of increasing the precision of the concept of fitness as well as making explicit this explanatory role that we now turn.

We have already seen that fitness is somehow connected with success at survival and reproduction, although it cannot be defined in terms of actual survival and reproductive success. Why have evolutionary biologists continued to confuse fitness with actual descendant contribution? We believe that the confusion involves a misidentification of the *post facto* survival and reproductive success of an organism with the *ability* of an organism to survive and reproduce. We believe that "fitness" refers to the ability. Actual offspring contribution, on the other hand, is a sometimes reliable—sometimes unreliable—indicator of that ability. In the hypothetical cases above, actual descendant contribution is clearly an unreliable indicator of descendant contribution capability. The identical twins are equally *capable* of leaving offspring. And the camouflaged butterfly is more *capable* of leaving offspring than is the non-camouflaged butterfly.

Thus, we suggest that fitness be regarded as a complex *dispositional* property of organisms. Roughly speaking, the fitness of an organism is its *propensity* to survive and reproduce in a particularly specified environment and population. A great deal more will have to be added before the substance of this interpretation becomes clear. But before launching into details, let us note a few general features of this proposal.

First, if we take fitness to be a dispositional property of organisms, we can immediately see how references to fitness can be explanatory.⁵ The fitness of an organism explains its success at survival and reproduction in a particular environment in the same way that the solubility of a substance explains the fact that it has dissolved in a particular liquid. When we say that an entity has a propensity

⁵Where fitness is defined as a propensity we can also squeeze the empirical content out of the phrase "survival of the fittest" (i.e., the claim that the fittest survive), which has frequently been claimed to be tautological (e.g., by Bethell 1976, Popper 1974, and Smart 1963. Just as the claim that "the soluble (substance) is dissolving" is an empirical claim, so the claim that those which could gain predominance in a particular environment are in fact gaining predominance, is an empirical claim. In short, to claim that a dispositional property is manifesting itself is to make an empirical claim. Such a claim suggests that the conditions usually known to trigger the manifestation are present, and no factors are present to override this manifestation. It seems plausible to interpret "the survival of the fittest" as a loose way of claiming that the organisms which are leaving most offspring are also the most fit. That this is a plausible interpretation of Darwin's use of the phrase is also suggested by Darwin's concern (in *The Origin of Species*) to demonstrate that conditions favoring natural selection are widely in effect. But it should be emphasized that nothing hinges on providing such an interpretation for "the survival of the fittest." This catch-phrase is not an important feature of evolutionary theory, in spite of the controversy its alleged tautological status has generated.

(disposition, tendency, capability) to behave in a particular way, we mean that certain physical properties of the entity determine, or are casually relevant to, the particular behavior whenever the entity is subjected to appropriate "triggering conditions." For instance, the propensity of salt to dissolve in water (the "water-solubility" of salt) consists in (i.e., "water solubility" *refers to*) its ionic crystalline character, which causes salt to dissolve whenever the appropriate triggering condition—immersion in water—is met. Likewise, the fitness of an organism consists in its having traits which condition its production of offspring in a given environment. For instance, the dark coloration of pepper moths in sooted, industrial areas of England effectively camouflages the moths from predators, enabling them to survive longer and leave more offspring. Thus, melanism is one of many physical properties which constitute the fitness, or reproductive propensity, of pepper moths in polluted areas (in the same sense that the ionic crystalline character of salt constitutes its propensity to dissolve in water).

The appropriate triggering conditions for the realization of offspring contribution dispositions include particular environmental conditions. We do not say that melanic moths are equally fit in polluted and unpolluted environments, any more than we claim that salt is as soluble in water as it is in mercury or swiss cheese.⁶

In addition to the triggering conditions which cause a disposition to be manifested, we must, in explaining or predicting the manifestation of a disposition, consider whether any factors other than the relevant triggering conditions were present to interfere with the manifestation. When we say that salt has dissolved in water because it is soluble in water, we assume the absence of disturbing factors, such as the salt's having been coated in plastic before immersion. Likewise, when we explain an organism's (or type's) offspring contribution by referring to its degree of fitness, we assume, for instance, that environmental catastrophes (e.g., atomic holocausts, forest fires, etc.) and human intervention have not interfered with the manifestation offspringing

⁶As this discussion suggests, an organism's fitness is not only a function of the organism's traits, but also of characteristics of the organism's environment. Actually, this function may be even more complicated. For evolutionary biologists have also noted that the fitness of an individual may depend upon the characteristics of the population to which it belongs. For instance, there is evidence of "frequency dependent selection" in several species of *Drosophila* (Kojima 1971). This kind of selection is said to occur whenever the fitness of a type depends upon the frequency of the type. Some types appear to be fitter, and are selected for, when they are rare. Thus, fitness is relative to environmental and population characteristics. And consequently, the appropriate triggering conditions for the realization of descendant contribution dispositions include environmental and population structure conditions.

contribution dispositions. In general, we want to rule out the occurrence of any environmental conditions which separate successful from unsuccessful reproducers without regard to physical differences between them.

Now let us fill in some of the details of this proposal. First, we must clarify the view of propensities we are presupposing. In our view, propensities are dispositions of *individual objects*. It is each hungry rat which has a tendency or propensity to move in the maze in a certain way; not the class of hungry rats. Classes—abstract objects, in general—do not have dispositions, tendencies, or propensities in any orthodox sense of the term.⁷ This aspect of propensities in general is also a feature of the (unexplicated) notion of fitness employed by biologists. Evolutionary biologists often speak of fitness as if it were a phenotypic trait—i.e., a property of individuals. For instance, Wallace (1963, p. 633) remarks, “That instances of overdominance exist, especially in relation to a trait as complex as fitness, is generally conceded.”

However, evolutionary biologists also employ a notion of fitness which refers to *types* (e.g., Dobzhansky 1970, pp. 101–102). Fitness cannot be a propensity in this case, although as we will argue, it is a derivative of individual fitness propensities. Thus, we will introduce two definitions of “fitness”: Fitness₁ of individual organisms and fitness₂ of types.

4.1 Fitness₁: Fitness of Individual Organisms. A paradigm case of a propensity is a subatomic particle’s propensity to decay in a certain period of time. Whether or not a particle decays during some time interval is a qualitative, nonrepeatable property of that particle’s event history. It might initially be thought that “propensity to reproduce” is also a qualitative nonrepeatable property of an organism: either it reproduces during its lifetime or it does not. However, the property of organisms which is of interest to the evolutionary biologist is not the organism’s propensity to reproduce or not to reproduce, but rather the *quantity* of offspring which the organism has the propensity to contribute. For, the evolutionary biologist is interested in explaining proportions of types in populations, and from this point of view, an organism which leaves one offspring is much more similar to an organism which leaves no offspring than it is to an organism which

⁷Given propensities apply to individual objects, (rather than chance set-ups or sequences of trials) we also take them to be ontologically real—not merely epistemic properties. Our view is similar to Mellor’s (for a good review of the views on propensities, cf. (Kyburg 1974), but it most closely follows Coffa’s analysis (1977, and his unpublished dissertation, *Foundations of Inductive Explanation*).

leaves 100 offspring. Thus, when we speak of “reproductive propensity,” this should be understood as a quantitative propensity like that of a lump of radioactive material (considered as an individual) to emit particles over time, rather than as a “yes-no” propensity, like that of an individual particle to decay or not decay during some time interval.

It may have struck the reader that given this quantitative understanding of “propensity to reproduce,” there are many such propensities. There is an organism’s propensity to leave zero offspring, its propensity to leave 1 offspring, 2 offspring, . . . , n offspring (during its lifetime). Determinists might claim that there is a unique number of offspring which an organism is determined to leave (i.e., with propensity 1) in a given environment. For non-determinists, however, things are more complicated. Organisms may have propensities of different strengths to leave various numbers of offspring. The standard dispositions philosophers talk about are tendencies of objects to instantiate certain properties invariably under appropriate circumstances. But besides such “deterministic” dispositions, there are the tendencies of objects to produce one or another of a distribution of outcomes with predetermined frequency. As Coffa (1977) argues, it seems just as legitimate to suppose there are such non-deterministic, “probabilistic” causes as to posit deterministic dispositions.⁸

If we could assume that there were a unique number of offspring which any organism is determined to produce (i.e., which the organism has propensity 1 to produce), then the fitness₁ of an organism could be valued simply as the number of offspring which that organism is disposed to produce. But since it is quite possible that organisms may have a range or distribution of reproductive propensities, as was suggested above, we derive fitness₁ values taking these various propensities into consideration.

Unfortunately, we also cannot simply choose the number of offspring which an organism has the *highest* propensity to leave—i.e., the mode

⁸While an organism has a number of different propensities to leave n offspring, for different values of n , we do not have the additional complication that an organism has a number of different propensities to leave a particular number of offspring, n . An object has many different *relative probabilities* to manifest a given property, depending on the reference class in which it is placed. (In practice, choice of reference classes is dependant on our knowledge of the statistically relevant features of the situation.) But an object’s *propensity* to manifest a certain property is a function of all of the casually relevant features of the situation, independent of our knowledge or ignorance of these factors. The totality of casually relevant features determines the unique correct reference class, and thus the unique strength of the propensity to manifest the property in question. (Thus it cannot be the case that an object has more than one propensity to manifest a particular property in a particular situation.)

of the distribution. For, in the first place, an organism may not have a *high* propensity to leave any particular number of offspring. In the second place, there may not be one number of offspring which corresponds to the mode of the distribution. For example, an organism might have a .5 propensity to leave 10 offspring and a .5 propensity to leave 20 offspring. And finally, even if there is a number of offspring which an organism has a significantly higher propensity to leave than any other number of offspring, we must take into account the remainder of the distribution of reproductive propensities as well. For example, an organism with a .7 propensity to leave 5 offspring and a .3 propensity to leave 50 offspring is very different from an organism with a .7 propensity to leave 5 offspring and a .3 propensity to leave no offspring, even though each has the propensity to leave 5 offspring as its highest reproductive propensity.⁹

In lieu of these considerations, one might suggest that the fitness₁ of an organism be valued in terms of the entire distribution of its reproductive propensities. The simplest way to do this is just to assign distributions as values. For example, the fitness₁ of an imaginary organism *x* might be the following distribution.

number of offspring	1	2	3	4	5	6	7	8	9	10
propensity	.05	.05	.05	.2	.3	.2	.05	.05	.05	

However, our intuitions fail us in regard to the comparison of such distributions. How can we determine whether one organism is fitter than another, on the basis of their distributions alone? For instance, is *x* fitter or less fit than *y* and *z*, whose distributions (below) differ from *x*'s?

number of offspring	1	2	3	4	5	6	7	8	9	10
<i>y</i>					1.0					
<i>z</i>			.5		.3					.2

In order to avoid the uncertainties inherent in this method of valuation, and still take into account all an organism's reproductive propensities, we suggest that fitness₁ values reflect an organism's *expected number* of offspring. The expected value of an event is the weighted sum of the values of its possible outcomes, where the appropriate weights are the probabilities of the various outcomes. As regards fitness₁, the event in question is an individual's total

⁹ It might initially be thought that these examples are highly artificial, since there are no such "bimodal" organisms. But organisms tend to have offspring in litters and swarms. For such organisms, their offspring contribution propensities will cluster around multiples of numbers typical of the litter or hatching size.

offspring contribution. The possible outcomes $0_1, 0_2, \dots, 0_n$ are contributions of different numbers of offspring. Values $(1, 2, \dots, n)$ of the outcomes correspond to the number of offspring left. And the weighting probability for each outcome 0_i is just the organism's propensity to contribute i offspring. Thus the imaginary organisms $x, y,$ and z above all have the same expected number of offspring, or fitness value, of 5.

We propose, then, that "individual fitness" or "fitness₁" be defined as follows:

The *fitness*₁ of an organism x in environment E equals $n = \sum p_i$ n is the expected number of descendants which x will leave in E .¹⁰

It may have occurred to the reader that the fitness values assigned to organisms are not literally propensity values, since they do not range from 0 to 1. But this does not militate against our saying that the fitness of an organism is a complex of its various reproductive propensities. Consider for comparison another dispositional property of organisms: their intelligence. If everyone could agree that a particular intelligence test really measured intelligence, then an organism's intelligence could be defined as the expected score on this test. (We would not value intelligence as the score actually obtained in a particular taking of the test, for reasons precisely analogous to those which militate against definitions of fitness in terms of actual numbers of organisms left. Intelligence is a competence or capacity of organisms, rather than simply a measure concept.) Obviously, intelligence would not be valued as the strength of the propensity to obtain a *particular* score. Similarly, it is the expected number of offspring which deter-

¹⁰ A note of clarification is in order concerning our definition of "fitness₁." It is not clear whether "expected descendant contribution" refers to expected offspring contribution, or expected second generation descendant contribution, or expected 100th generation descendant contribution. The problem can be illustrated as follows. One kind of individual may contribute a large number of offspring which are all very well adapted to the environment into which they are born, but cannot adapt to environmental changes. As a result, an individual of this type contributes a large number of offspring at time t , but due to an environmental change at $t + \Delta t$, these offspring in turn leave very few offspring, so that the original individual actually has very few second or third generation descendants. On the other hand, individuals of an alternate type may leave fewer offspring, yet these offspring may be very adaptable to environmental changes. Thus, although an individual of the latter type contributes a lower average number of offspring at time t , that individual may have a greater descendant contribution at $t + \Delta t$. Which individual is fitter? We suggest differentiating between long term fitness and short term fitness—or between first generation fitness, second generation fitness, . . . , n -generation fitness. Thus, the latter type is fitter in the long term, while the former is fitter in the short term.

mines an organism's fitness values, not the strength of the propensity to leave a particular number of offspring.

4.2. Fitness₂: Fitness of Types. Having defined fitness₁, we are in a position to define the fitness₂ of types. As will become apparent in what follows, it is the fitness of types which figures primarily in explanations of microevolutionary change.

Intuitively, the fitness of a type (genotype of phenotype) reflects the contribution of a particular gene or trait to the expected descendant contribution (i.e., the fitness₁) of possessors of the gene or trait. Differences in the contributions of alternate genes or traits would be easy to detect in populations of individuals which were phenotypically identical except in regard to the trait or gene in question. In reality, though, individuals differ with regard to many traits, so that the contribution of one or another trait to fitness₁ is not so straightforward. In fact, the notion of any simple, absolute contribution is quite meaningless. For a trait acts in conjunction with many other traits in influencing the survival and reproductive success of its possessors. Thus, its contribution to different organisms will depend upon the different traits it is associated with in those organisms.

Yet, in order to explain the evolution and/or persistence of a gene or its phenotypic manifestation in a temporally extended population, we would like to show that possessors of the gene or trait were generally better able to survive and reproduce than possessors of alternate traits or genes. (By "alternate genes" we mean alternate alleles, or alternate genes at the same locus of the chromosome. "Alternate traits" are phenotypic manifestations of alternate genes.) In other words, we want to invoke the *average* fitness₁ of the members of each of the types under consideration. Let us refer to average fitness₁ as "fitness₂." Given some information about the fitness₂ of each of a set of alternate types in a population, and given some information about the mechanisms of inheritance involved, we can predict and explain the evolutionary fate of the genes or traits which correspond to the alternate types. For instance, if we knew that possessors of a homozygous-based trait were able to contribute a higher average number of offspring than possessors of any of the alternate traits present in the population, we would have good grounds for predicting the eventual predominance of the trait in the population.

As the above discussion suggests, we actually invoke *relative* fitness₂ values in predictions and explanations of the evolutionary fate of genes and traits. That is, we need to know whether members of a particular type have a *higher* or *lower* average fitness₁ in order to predict the fate of the type. In order to capture this notion, and

to accommodate biologists' extensive references to "relative fitness" or "Darwinian fitness," we introduce "relative fitness₂." Given a set of specified alternate types, there will be a type which is fittest in the fitness₂ sense (i.e., has highest average fitness₁, designated "Max Fitness₂"). Using this notion of Max Fitness₂, we define relative fitness₂ as follows:

The relative fitness₂ of type X in E
 $=_{df}$ the fitness₂ of X in E / Max fitness₂ in E

The role of relative fitness₂ ascriptions in evolutionary explanations has been acknowledged (for instance by Williams' "condition 3" in her analysis of functional explanations (1976)). Yet very little attention has been paid to the establishment of these ascriptions. Perhaps we should say a few words about these claims. For it might be supposed that the *only* way in which fitness₂ ascriptions can be derived is through measurements of actual average offspring contributions of types. If this were the case, even though "fitness₂" is not *defined* in terms of such measures (so that explanations employing fitness₂ ascriptions to explain actual offspring contribution differences would not be formally circular), claims concerning the influence of fitness₂ differences upon offspring contribution could not be *tested*. This would obviously be disastrous for our analysis.

Evolutionary biologists frequently *derive* relative fitness claims from optimality models (e.g., Cody 1966); this is basically an engineering design problem. It involves determining, solely on the basis of design considerations, which of a set of specified alternate phenotypes maximizes expected descendant contribution. The solution to such a problem is only optimal relative to the other *specified* alternatives (there may be an unspecified, more optimal solution). Thus, optimality models provide some insight into the relative fitness of members of alternate types.

The theorems derived from optimality models can be confirmed by measurements of actual descendant contribution. Such measures can also be used to generate fitness₂ ascriptions. Given evidence that descendant contribution was affected primarily or solely by individual propensities for descendant contribution, we can infer that descendant contribution measurements are indicative of individual or type fitness.

4.3 Explaining Microevolutionary Phenomena. Having elaborated the notions of fitness₁ and relative fitness₂, we hope to show how these concepts function in explanations of evolutionary phenomena. Perhaps the clearest means of showing this is to work through an example

of such an explanation. The example we are going to consider involves a change in the proportion of the two alleles at a single chromosomal locus, and a change in the frequency of genotypes associated with this locus, in a large population of organisms. In this population, at the locus in question, there are two alleles, A and a . A is fully dominant over a , so that AA and Aa individuals are phenotypically indistinguishable with respect to the trait determined by this locus. This trait is the "natural gun" trait. All individuals which are either homozygous (AA) or heterozygous (Aa) at this locus have a natural gun, whereas the unfortunate individuals of genotype aa have no gun. Let us suppose that for many generations this population has lived in peace in an environment E , in which no ammunition is available. (Were the terminology not in question, we would say that there had been no "selective pressure" for or against the natural gun trait.) However, at generation n , environment E changes to environment E' , by the introduction of ammunition usable by the individuals with natural guns. At generation n , the proportion of A alleles is .5 and the proportion of a alleles is .5, with the genotypes distributed as follows:

$$AA: .25 \quad Aa: .50 \quad aa: .25$$

What we want to explain is that in generation $n + 1$, the new frequency of genotypes is as follows:

$$AA: .29 \quad Aa: .57 \quad aa: .14$$

Let us suppose that the large size of this population makes such a change in frequency extremely improbable ($p = .001$) on the basis of chance.

We need two pieces of information concerning this population in order to explain the change in frequency. We need to know (1) the relative fitness₂ of the natural gun and non-natural gun types, and (2) whether any conditions obtain which would interfere with the actualization of the descendant contribution propensities which the relative fitness₂ valuations reflect. As was noted above, the fact that an organism does not survive and reproduce in an environment in which periodic cataclysms occur is no indication of its fitness (any more than the failure of salt to dissolve in water when coated with plastic would count against its solubility).

The latter qualification, stating that no factors other than fitness₂ differences were responsible for descendant contribution, corresponds to the "extremal clause," which, as Coffa (1977, p. 194) has made clear, is a component in the specification of most scientific laws. Such clauses state that no physical properties or events relevant to

the occurrence of the outcome described in the law (other than those specified in the initial conditions) are present to interfere with that outcome. In stating scientific laws, the assumption is often tacitly made that no such disturbing factors are present. But as Coffa has pointed out, it is important to make this assumption explicit in an extremal clause. For, no scientific law can be falsified by an instance in which the event predicted by the law fails to occur, unless the extremal clause is satisfied. Thus, our ability to fill in the details of the extremal clause will determine our ability to distinguish between contexts which count as genuine falsifications of a law and contexts which do not. The fact that evolutionary theorists are fairly specific about the types of conditions which interfere with selection is an indication in favor of the testability of claims about fitness. As noted above, the influence of fitness upon offspring contribution is disturbed by any factors which separate successful from unsuccessful reproducers without regard to physical differences between them. In addition, certain other evolutionary factors such as mutation, migration, and departures from panmixia may disturb the systematic influence of fitness differences between types upon proportions of those types in subsequent generations.

Let us suppose that we do know the relative fitnesses₂ of the natural gun and non-natural gun types, and let us suppose the natural selection conditions are present (i.e., nothing is interfering with the manifestation of the fitness propensities). This information together with the relevant laws of inheritance will allow us to predict (and explain) the frequencies of types in generation $n + 1$. We need not detail the principles of inheritance which allow this computation here (since they are available in any genetics text) other than to note that the Hardy-Weinberg Law allows us to compute the relative frequencies of types in a population, given information about the heritability of the types in question together with hypotheses about fitness₂ differences.

In light of these considerations, we construct the promised schema as follows:

1. In E' , in generation n , the distribution of genotypes is:

$$AA: .25 \quad Aa: .50 \quad aa: .25$$

2. $(x)(AAx \supset tx) \ \& \ (x)(Aax \supset tx) \ \& \ (x)(aax \supset -tx)$
3. In E' , the relative fitness₂ of type t is 1.0.
4. In E' , the relative fitness₂ of type not- t is 0.5.
5. For any three distinct genotypes X, Y, Z (generated from a single locus), if the proportions of X, Y, Z in generation n

are P , Q and R , respectively, and if the relative fitnesses₂ of genotypes X , Y , and Z are $F(X)$ and $F(Z)$, respectively, then the proportion of X in generation $n + 1$ is:

$$P \cdot F(X) / P \cdot F(X) + Q \cdot F(Y) + R \cdot F(Z)$$

6. $EC(E)$

7. Given the size of population P , the probability that the obtained frequencies were due to chance is less than .001.

.99

In E' at generation $n + 1$ the frequency of genotypes is:

$$AA : .29 \quad Aa : .57 \quad aa : .14$$

This explanation is of the inductive-statistical variety, with the strength of the connection between explanans and explanandum determined, as indicated in premiss (7), by the size of the population. Premiss (1) is, obviously, a statement of the initial conditions. Premiss (2) allows us to determine which genotypes determine each phenotype: all individuals with genotype AA or Aa have trait t , and all individuals of genotype aa lack trait t . Premises (3) and (4) indicate the relative fitness₂ of types t and not- t in environment E . Premiss (5) is the above-mentioned consequence of the Hardy-Weinberg Law which allows computation of the expected frequencies in generation $n + 1$, given information about reproductive rates at generation n , together with information about initial frequencies of individuals of each genotype at generation n . Premiss (6) affirms that the extremal clause (EC) was satisfied—i.e., that the “natural selection conditions” were present for the environment (E) in question. Thus we can infer that propensities to contribute descendants will be reflected in actual reproductive rates. Each genotype receives the relative fitness₂ associated with the phenotype it determines, as indicated in premiss (2). Thus by substitution of the values provided in premises (3) and (4) in formula (5) (i.e., $X = AA$, $F(X) = 1.0$, $P = .25$; $Y = Aa$, $F(Y) = 1.0$, $Q = .50$, . . . etc.) we can obtain the values which appear in the explanandum.

To summarize, from knowledge of (1) initial frequencies of genotypes in generation n , (2) the relative fitness₂ of those genotypes, and (3) the fact that the extremal clause was satisfied, we can infer what the frequencies of genotypes will be in generation $n + 1$.

Of course, in this admittedly artificial example, it was presumed that the appropriate relative fitness₂ values were known. This suggests that we somehow investigated reproductive *capabilities*, and not just reproductive differences. We must emphasize, however, that actual reproductive differences may be regarded as measures of differences

in reproductive capability, as long as *the measured differences are statistically significant*. This is the means of fitness determination in many, if not most, evolutionary investigations. But this must not mislead the reader into identifying fitness with actual reproductive contribution. For *statistically significant* differences would not be required to establish fitness differences in this case. Rather, statistically significant differences are required to establish that certain variables (fitness differences, in this case) are causally connected with other variables (in this case, differences in offspring contribution). Statistically significant differences are thus quite appropriate measures for fitness differences, given the propensity interpretation of fitness.

Having explained the role of statistical significance in measuring fitness differences, we can now consider a more realistic example of the role of fitness in population biology. Certainly one of the greatest controversies in the history of population genetics concerns the differences in fitness of heterozygotes and homozygotes. The importance of the controversy lies in the fact that if heterozygotes are generally fitter than homozygotes, then breeding groups will retain a greater amount of genetic variation than if homozygotes were generally superior in fitness. And the amount of variation present in a population is of considerable importance to the evolutionary fate of the population. (For instance, greater variation provides some "flexibility" in the sense that a genetically variable population has more alternatives for adapting to changing environmental conditions.) Theodosius Dobzhansky, a principal protagonist in this controversy, maintained that heterozygotes at many loci were fitter than homozygotes at the same loci, and he and his collaborators gathered a good deal of statistically significant data to support this contention.

For instance, in one article, it was reported that members of the species *Drosophila pseudoobscura* which were heterozygous in regard to the structure of their third chromosome were more viable than the flies which were homozygous. Dobzhansky et. al. correlated viability differences (note that *viability* differences are dispositional property differences) with fitness differences, and they performed a statistical analysis on their data, in order to conclude that:

Heterosis [heterozygote superiority in fitness] has . . . developed during the experiment, as indicated by the attainment of equilibrium and by a study of the viability of the flies derived from the cage. Both tests gave statistically significant results. (1951, p. 263)

Again, statistical significance would be of no concern if fitness were identified straightforwardly with offspring contribution. Statistical significance is important, however, if fitness is identified with phen-

otypic properties causally connected with offspring contribution.

As these examples demonstrate, fitness ascriptions play not only a legitimate, but a crucial role in explanations of evolutionary change. While biologists have not been able to justify their usage of the concept of “fitness,” their usage of that concept has nevertheless been consistent and appropriate. Philosophers have accused biologists of giving circular explanations of evolutionary phenomena because they have only taken into account the definitions of fitness biologists explicitly cite, and they have not looked for the interpretation implicit in biologists’ usage.

4.4 A Propensity Analysis of Natural Selection. One consequence of our propensity interpretation of fitness is that the analysis also points to an improved definition of “natural selection.” As was noted earlier, the concepts of fitness and natural selection are inextricably bound—so much so that misinterpretations of fitness are reflected in misinterpretations of natural selection.

Thus, according to one of the more popular interpretations of natural selection, that process occurs whenever two or more individuals leave different numbers of offspring, or whenever two or more types leave different average numbers of offspring. For example, Crow and Kimura (1970) stipulate that,

“Selection occurs when one genotype leaves a different number of progeny than another.” (p. 173)

Insofar as it is correct to say that the *fittest* are *selected*, this definition of “selection” clearly reflects a definition of “fitness” in terms of actual descendant contribution.

But surely these definitions (see also Wallace, (1963, p. 160); Wilson, (1975, p. 489)) do not adequately delimit the reference of “natural selection.” For evolutionary biologists do not refer to just any case of differential offspring contribution as “natural selection.” For instance, if predatory birds were to kill light and dark-colored moths indiscriminately, and yet by chance killed more light than dark ones, we would not attribute the differential offspring contribution of light and dark moths to natural selection. But if the dark coloration acted as camouflage, enabling the dark moths to escape predation and leave more offspring, we would attribute the resulting differential offspring contribution to the action of natural selection. For only in the latter case are differences in offspring contribution due to differences in offspring contribution dispositions.

Thus, Kettlewell (1955, 1956) did not presume to have demonstrated the occurrence of natural selection simply by pointing out the dramatic

increase in frequency of dark-colored pepper moths within industrial areas of England. In order to demonstrate that selection (*vs.* chance fluctuations, migration, etc.) had accounted for the change, Kettlewell had to provide evidence that the dark-colored moths were better able to survive and reproduce in the sooted forests of these regions. Nor did Cain and Sheppard (1950, 1954) and Ford (1964) consider differential contribution to be a sufficient demonstration of natural selection in their celebrated accounts of the influence of selection on geographical distribution. In order to support the hypothesis that natural selection had affected the geographic distribution of various color and banding-pattern traits of snails of the species *Cepaea nemoralis*, these men argued that the colors and band-patterns peculiar to an area were correlated with the background color and uniformity of that area. More precisely, yellow snails were predominant in green areas; red and brown snails were predominant in beechwoods (“ . . . with their red litter and numerous exposures of blackish soil . . . ” (Ford 1964, p. 153)); and unbanded shells were predominant in more uniform environments. These traits effectively camouflaged their possessors from the sight of predators (Ford, 1964, p. 155), thus *enabling* suitably marked snails to contribute more offspring than the unsuitably marked snails.

In each of these cases, selection is construed as involving more than just differential perpetuation. Rather, selection involves differential perpetuation caused by differential reproductive capabilities. So, just as we amended traditional definitions of “fitness” to take into account descendant contribution propensities, we must also amend traditional definitions of “selection” so as to emphasize the role of differential descendant contribution propensities. Selection, properly speaking, involves not just the differential contribution of descendants, but a differential contribution *caused* by differential propensities to contribute. On the basis of these considerations, let us define “individual selection” and “type selection” as follows:

Natural selection is occurring in population P in environment E with regard to organisms x, y, z (members of P) =_{df} x, y, z differ in their descendant contribution dispositions in E , and these differences are manifested in E in P .

Natural selection is occurring in population P in environment E with regard to types X, Y, Z (included in P) =_{df} members of X, Y, Z types differ in their average descendant contribution dispositions in E , and these differences are manifested in E in P .

We know from our previous analysis that when organisms leave

numbers of offspring which reflect their reproductive propensities (i.e., when reproductive propensities are manifesting themselves) in a particular environment, this implies that no factors are interfering with the manifestation of these propensities. (cf. our remarks on extremal clauses above). Put more positively, we have grounds for believing that, for example, no cataclysms, cases of human intervention, etc., are occurring. Of course, the occurrence of natural selection is not precluded by the incidence of such factors. Fitter individuals might leave more offspring than less fit individuals (on account of their fitness differences), even though non-discriminating factors are operating to minimize the reproductive effects of fitness differences. In other words, the incidence of non-discriminating factors will not necessarily override the effects of fitness differences. Thus, we do not have to rule out the occurrence of non-selective factors in our definition of "natural selection." But in explanations (such as our Hempelian schema above) of the precise evolutionary effects of selection, we must take these non-selective factors into account.

5. Conclusion. A science may well progress even though its practitioners are unable to account for aspects of its foundations in any illuminating way. We believe that this has been the case with evolutionary theory, but that the *propensity* analysis of fitness which we have described captures the implicit content in biologists' usage of the term. The propensity interpretation allows us to reconstruct explanations of microevolutionary phenomena in such a way that these explanations appear to be entirely respectable and noncircular. By their form, and by inspection of the premises and conclusion, such explanations appear to satisfy Hempelian adequacy requirements for explanations, and even appear to incorporate recent modifications of the Hempelian model for inductive explanations (Coffa 1974). We chose an example of microevolutionary change, since we wanted the least complicated instance possible in order to illuminate the form of explanations utilizing fitness ascriptions. We know of no reason to believe that a similar reconstruction could not be given for the case of macroevolutionary change.¹¹

¹¹ A great deal more needs to be done by way of clarifying the concepts of fitness and natural selection, given the many uses biologists make of these concepts. But we believe that the broad analyses we have given provide an adequate framework within which further distinctions and clarifications can be made. For example, within the categories of fitness₁ and relative fitness₂, distinctions can be drawn between short and long term fitness, by distinguishing between propensities to leave descendants in the short run (in the next few generations) vs. propensities to leave descendants in the long run (cf. footnote 7).

The propensity interpretation also lends itself to the much-discussed notion of

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"frequency dependent fitness," wherein the fitness of a type differs according to the frequency of the type. Certain cases of mimicry have been explained via reference to frequency dependent fitness. For instance, it has been suggested that the mimetic resemblance of a prey species to a distasteful model may enhance the survival of the mimics so long as they are rare, because individual predators most readily learn to avoid the distasteful type (and hence the mimic) when the model is more common than the mimic. Surely the survival *ability* of the mimics, and not just their survival rates, are enhanced by the scarcity of their type.

The sociobiological notion of "inclusive fitness" also seems susceptible to a propensity analysis. Biologists have invoked this notion in order to explain the evolution of certain altruistic traits. The idea (very simply) is that some of the organisms benefitting from an altruistic action may be genetically related to the altruistic actor, and may therefore share the behavioral trait which led to the action (if the trait is genetically-based). Thus, although an altruistic action may decrease the fitness₁ of the actor, it may increase the fitness₂ of the altruistic trait. As a result, the trait may come to predominate within the population. "Inclusive fitness" values have been proposed as appropriate indicators of the evolutionary fate of altruistic traits. These values take into account not only the effect of altruistic actions upon the fitness of the actors, but also the probability that the action will benefit genetic relatives, and the extent of the benefit to relatives (cf. Hamilton 1964). Our colleague Greg Robischon is currently considering a propensity interpretation of inclusive fitness.

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