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A Defense of Propensity Interpretations of Fitness¹

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1. Introduction: Probabilities and Propensities in Fitness

That there was *some* chance element to evolutionary change was clear even to Darwin (cf. Hodge 1987; also Hodge & Kohn 1986), but chance has assumed a more central role in evolutionary theory since the early decades of this century. It was certainly clear to theoreticians such as Dobzhansky, Wright and Fisher that an adequate evolutionary theory would have to take a stochastic form, though they disagreed as to the significance of chance in evolution (Gigerenzer et al., 1989, ch. 4; Turner 1987). As Beatty explains, the central difference is that in more modern treatments, not only is the *origin* of variations a matter of chance, their evolutionary *fates* are also matters of chance (Beatty 1984; cf. Beatty 1987). Probabilistic theories of evolutionary change, as we shall be concerned with them, emphasize this dependency of evolutionary fates on chance, and treat evolutionary change as irreducibly probabilistic.

In recent philosophical literature on the topic, the dependence of evolutionary fates on chance has often led to a treatment of fitness as probabilistic and, in particular, as a propensity. On propensity interpretations, "... the fitness of an organism is its *propensity* to survive and reproduce in a particularly specified environment and population" (Mills and Beatty 1979, p. 42). Alternatively, "... the (relative) expected fitness of a type of organism as compared with specific competitors in a specified environment is its propensity to manifest a certain (relative) rate of reproductive success as compared with those competitors" (Burian 1983, p. 301). Propensities are natural dispositions which can be manifested in long term frequencies; they help explain the actual observed frequencies within a domain. As a propensity, fitness would be a natural disposition manifested in long term reproductive differences, useful for explaining actual differences in survival and reproduction. With fitness, understood as *expected reproductive success*, natural selection becomes differential reproduction due to fitness differences. So understood, propensity interpretations of fitness are critically tied to an acknowledgment of the probabilistic character of evolutionary change, and also to a particular interpretation of probability.

Representing fitnesses, or fitness differences, as probabilistic quantities has several *prima facie* advantages. Any treatment of fitness will need to maintain these advan-

tages, whether or not the account is probabilistic. First, such representations allow us to distinguish fitness from actual reproductive success, or what we often will call *realized fitness*.² Actual reproductive success can deviate significantly from what would be expected on the basis of fitness assignments. Equally fit organisms can differ in their actual reproductive success, and less fit organisms can out-reproduce more fit organisms; indeed, if we consider an array of cases with intermediate fitness values, we should *expect* less fit organisms to prevail at least sometimes. Any given level of reproductive success is, except in the limiting cases, consistent with any fitness assignment. One principled way of motivating the distinction between expected and realized fitness is embedding fitness within a probabilistic framework.

Second, probabilities seem to be pitched at an appropriate level of generality for evolutionary explanations. Phenotypic or genotypic properties which are otherwise quite different can result in the same level of fitness; as Rosenberg puts it, "... there are many different ways in which the same level of fitness may be possessed, and there is consequently no one-to-one relation between a given level of fitness and a manageable set of its causal conditions" (1983, p. 459). This dependence of fitness on phenotypic or genotypic properties is what he means by "supervenience." There is no manageable characterization of the phenotypic or genotypic properties on which a given level of fitness supervenes; that is, no disjunction of phenotypic or genotypic properties, however heterogeneous, will yield a general characterization of fitness differences. In this respect, fitness assignments abstract from phenotypic and genotypic details, while depending on them. Even though phenotypic differences can explain differences in fitness within populations and even though fitness supervenes on phenotypic differences, there can be no general characterization of fitness in terms of phenotypic differences (cf. Brandon 1990, ch. 1).

Third, probabilistic analyses of fitness promise to clarify the crucial distinction between the effects of selection and those of drift in evolution. Genetic drift—essentially, sampling error due to small population size—can result in differential reproduction and therefore in evolutionary change. We will see that this issue is vexed in a number of ways. Brandon (1990, p. 9) says that though natural selection and drift both occur in actual populations, "drift and natural selection are alternatives", each capable of explaining differential reproduction. Similarly, Falconer (1989) treats selection and drift as different "agencies" through which the genetic properties of a population may be changed. An adequate account of fitness must provide a conceptually satisfactory distinction between drift and selection.³ This is a corollary of the first point above; for, as Beatty explains, if fitness is identified with *actual* reproductive success, "... the distinction between random drift and natural selection of the fittest dissolves, and along with it dissolves the issue of the relative evolutionary importance of the two supposedly different sorts of processes" (1984, p. 191).

We shall emphasize the interpretation of fitness within a general account of evolution. We will deal only with a limited fragment of evolutionary theory, neglecting a variety of factors affecting evolutionary change, including developmental constraints and factors affecting the origin of variation. There are a number of important issues even within the narrower fragment which we will not address directly, but which are clearly relevant to evaluating the adequacy of an interpretation of fitness. First, we will not discuss the level at which selection acts (cf. Brandon 1982; Kane et al., 1990; Sober 1992). For convenience, we shall treat selection as if it occurred at the level of organisms, acting on the phenotype. While this is obviously a common case, we do *not* presuppose that this is the only level at which selection acts, or that there is only one such level. Indeed, a general account of fitness should apply at many levels, but we will set this issue aside. Accordingly, we will concentrate on selection over a gen-

erational time scale, changing the means, variances, and covariances of phenotypic distributions. Second, it is important to discriminate different propensities, distinguishing a propensity for reproduction from, for example, a propensity for survival, or within the former, distinguishing mating success from viability and fecundity. It is theoretically important to distinguish the various components of fitness (cf. Arnold and Wade 1984a, 1984b; also Prout 1971a, 1971b); an account that did not allow one to discriminate between them would be inadequate. Finally, we will assume the relativity of fitness to both the biotic and the abiotic environment. It is allowed on all hands that fitness is relative to the environment, even though there is in point of fact no entirely general way of accommodating this relativity in most models. We believe that a propensity interpretation can handle these issues.

Many discussions of the propensity interpretation fail to be responsive to the sources of probabilistic components in evolution and the various problems concerning the interpretation of probability. We intend to take such issues seriously in discussing propensity interpretations. In Part 2I, we will turn to the *probabilistic* character of evolutionary change under selection and drift, and will isolate the peculiar role of fitness values in probabilistic models of evolutionary change. In Parts 3 and 4, we will turn to the commitment to *propensity interpretations* as opposed to other interpretations available for understanding fitness as probabilistic, including in particular appeals to limiting frequencies.

2. Fitness as a Probabilistic Quantity

Realized fitness cannot suffice to *define* fitness: "... in any *single* run organisms of the relatively fittest type may not out-reproduce their competitors; indeed, there are occasionally cases in which none of the fittest organisms survive" (Burian 1983, p. 301). Sober uses the following analogy to explain the role of statistical information in estimating fitness levels. Tossing coins provides relevant *evidence* concerning whether the coins are biased. If three coins are thrown, one a million times, one three times, and one never, they will obviously differ in the *actual* frequencies of heads thrown even though they may have the same *probability* of coming up heads. As Hacking says,

If we take seriously the notion of objective possibility, feasibility, proclivity, propensity, or whatever we call it, such degrees of feasibility may themselves be objects of knowledge, to be known with varying degrees of precision. (1975, p. 128)

Fisher, in his work on statistical theory, thought of frequencies as defined in "hypothetical infinite populations", and the actual data as a random sample from those infinite populations (1938; cf. Hacking 1965). Objective probabilities are objects of knowledge, known more or less completely, supported by evidence with varying degrees of sensitivity; the actual data provide some evidence to assess probabilities. The fitness of phenotypes does not depend, as such, on how often they occur, any more than the bias of a coin depends on how often it is tossed; neither can the fitness of phenotypes be defined in terms of the actual changes of frequencies within populations. "Populations of different sizes and compositions may be characterized by the same set of fitness values, just as coins that differ in the number of times they are tossed may have the same bias" (Sober 1984a, p. 43). From such considerations, Sober concludes that fitness is a "probabilistic quantity", and Brandon that "natural selection is a statistical phenomenon" (1978, pp. 69-70).

The precise sense in which fitness is a probabilistic quantity, or a statistical phenomenon, often has been misunderstood or misdescribed. It is not always transparent what advocates take the proposed propensities to consist in. Beatty suggests that the

environment is specified by a “range of circumstances, each weighted according to the likelihood of its occurrence” (1984, p. 193). In each environment, a phenotype will have a definite fitness, and the phenotype can be regarded as having a range of offspring contributions depending on the specific circumstances it encounters. Different probabilities for reproduction, or survival, are a consequence of the different probabilities of encountering specific circumstances, and this alone is the source of the probabilistic character of fitness functions. In May’s (1973, ch. 5) deterministic models, it is possible to find constant equilibrium values for, say, two-species systems, and these equilibrium values will be points; but when the environment varies temporally, equilibrium values will vary as well and these values must be represented as probability distributions. The probabilistic character of fitness in such cases is a consequence of the environmental relativity of fitness, and of the uncertainties of environmental variation. In other interpretations of fitness as a propensity, what seems to be contemplated is more radical, taking fitness itself as a probabilistic function, so that, even in a uniform environment and in the absence of drift, the consequences of selection would be “statistical” or “probabilistic” (e.g., Brandon 1990, Burian 1983, Sober 1984a). That is, a fitness function would itself be a function from a phenotypic frequency to an array of frequencies which describe the possible outcomes after selection.⁴

The role of fitness within a probabilistic evolutionary framework can be clarified by examining the relationship of random drift and selection. Let us grant for the sake of argument that fitness is a supervenient property; that is, that fitness depends only upon “the manifest properties of organisms—their anatomical, physiological, and behavioral properties—right down to their molecular constituents and their interaction with physical properties of the environment” (Rosenberg 1985, p. 165).⁵ Fitness will be “objective” in the sense that it is a real and measurable feature of organisms. Yet there will be no “manageably small” number of manifest properties in terms of which a particular fitness level can be defined. Fitness of *types* may still be a statistical property; for example, we may identify the fitness of a phenotype or genotype with the mean value of the realized values for individuals. This is suggested by Sober’s comment that

Evolutionary theory understands fitness as a probabilistic quantity. An organism’s fitness ... is its *chance* of surviving. A genotype’s fitness is the average of the relevant probabilities attaching to the organisms who have that genotype. The genotypic fitnesses are survival probabilities, which is to say that they represent the average chance an organism of a given type has of surviving from egg to adult. (1984a, p. 43)

Sober’s claim must be understood with care. His discussion is not altogether transparent. It could be understood as defining fitness by a simple frequentist averaging procedure (Horan 1991); however, we think it is better read in terms of models of fitness in infinite ensembles of populations, as described below.

Evolution is certainly a matter of chance. Genetic drift is simply the “error” in transmission of types from generation to generation, arising from finite population size. Drift is standardly treated using models incorporating infinite, or effectively infinite ensembles of finite populations. Given a single gene with two alleles, in the absence of selection ensembles of populations initially polymorphic at that locus will tend to disperse across a wide range, from populations fixed for one allele to populations fixed for the alternative allele (see Falconer 1989 or Roughgarden 1979). Once a population is fixed for one allele, it will not change unless there is significant mutation. The extremes are therefore absorbing states, from which populations will not deviate. The end result will be that, as the ensemble disperses, each population will tend to be monomorphic. In the limit, the ensemble of populations will bifurcate into

a bimodal distribution at the two extremes. (For experimental confirmation, see Kerr and Wright 1954.)

The rate at which this dispersion occurs will depend critically on N_e , the effective population size. The overall effects will be diffusion of populations in the ensemble, differentiation between populations, and uniformity within populations. This is a *neutral* case, in which there are no relative selective advantages. Selection, by contrast, is treated in these models as a *deterministic* process; that is, if selection were the *only* force operating, then a given frequency within a population at one time will yield a unique distribution of frequencies in the next generation. This is expressed mathematically by supposing that we have infinite or effectively infinite populations, in which sampling error, and therefore drift, could not occur. In these cases, the change in \bar{z}_t , the mean value of some phenotypic trait z at time t , will be

$$\Delta\bar{z}_t = \bar{z}_{t+1} - \bar{z}_t = h^2\sigma^2(s\bar{z}_t - \bar{z}_t),$$

where \bar{z}_t is the mean value of z in generation t (before selection), s the selection coefficient, and $h^2\sigma^2$ the heritable variance. In an infinite population, these changes would *always* be a deterministic function of fitness and will *always result in an increase in fitness as a function of the selection differential and heritable variance in fitness*. Changes in fitness will be a function of the local adaptive topography. When confronted with finite populations (cf. Lande 1976; Wright 1931, 1932), drift is incorporated as the random exploration of adaptive zones; that is, drift is expressed as changes in frequencies that are *uncorrelated* with differences in fitness, or random with respect to selection (Beatty 1984). Drift would change the frequencies within populations in an infinite ensemble, but should leave the mean value of the distribution in the ensemble unchanged from the initial value, in the absence of directional selection.⁶ Thus, the *variance* of the ensemble would change, though the *mean* would not. Fitness values will determine the strength and location of the central tendency within the ensemble, and the amount of drift will be seen as the amount of dispersal around that mean value. It is *only* in this sense that the fitness of a genotype or phenotype is given by the average chance of survival: drift alone will not change the *mean* value in an ensemble of populations, though it *will* change the variance.⁷

The general point is then rather simple. Fitness, as modeled in infinite populations with uniform environments, is strictly a deterministic function. Understood as a consequence law (cf. Sober 1984a), in infinite populations it allows a simple deterministic prediction of frequencies from one generation to the next, and even in ensembles of finite populations allows a unique prediction of the expected mean value (though the variance is a function of stochastic variation). Selection is *not* strictly a probabilistic process, but a deterministic component *within* a stochastic process. Fitness functions yield unique mappings from prior to subsequent frequencies, with absolute fitness increasing in proportion to differences in fitness when the population is not yet at an equilibrium state. There may be stochastic effects due, for instance, to drift and the result is an evolutionary process that is stochastic, but the effects of selection are not probabilistic. Likewise, the fitness of a phenotype may be represented as an array of values, as it is by Beatty and Finsen, depending on the likelihood of encountering various environments, and thus be a probabilistic function in a heterogeneous environment. In this case, the stochastic component to the evolutionary process follows directly from the grainy character of the environment, and the environmental relativity of fitness.

The case is more complicated in finite populations, for a number of reasons. Since there cannot be continuous variation of frequencies in such populations, there is generally significant rounding error; this means that the mathematical models discussed

above have no univocal application. This effect will be compounded by the inevitability of drift and associated phenomena such as variance in heritability. It might be tempting to think that once we descend from the level of mathematical abstractions, we will find more fundamental sources for the probabilistic character of fitness. Perhaps so, but neither of us knows of any cases in which this is clearly so. In either case, the view that simply shifting to a finite population requires a probabilistic treatment for fitness is a mistake.

The point can be seen by turning to some simple models of population growth to explore the consequences of finite population size. All assume a homogeneous environment. In deterministic exponential models,⁸ population increases as a simple exponential function over time. With stochastic effects introduced—for example, from environmental variance—the population dynamics yields an array of values. An actual growth curve may lie above or below the value predicted on the simple exponential models. The exponential curve reflects what is commonly called the *intrinsic rate of increase* or the *Malthusian parameter*. This represents what would be predicted on the basis of reproductive rates alone. The stochastic array is a function of the variance induced by the environment. Analogously, consider a case of simple directional selection, with complete dominance and selection against one homozygote. In the deterministic case, we have a simple exponential decay representing the changing expected frequencies. With stochastic effects introduced—for example, drift with a small population size—we obtain an array of values. An actual, finite, population may experience changes under selection which lie above or below the value predicted on the simpler model. The effect of selection, however, is still to define the *expected* value, or the *intrinsic* effects due to selection. Again, this is what would be predicted in the absence of drift. The variance is not due to selection, but to drift. By itself, the shift to finite population size provides no motivation for treating fitness as a probabilistic function. When N_E is finite, the *realized* fitness will vary stochastically and the variance will be inversely related to N_E . As N_E becomes very large, the variance will approach zero, and evolutionary change will approximate the deterministic limit. As N_E becomes smaller, the effects of drift become more pronounced, and may dominate selection. Nonetheless, even in this finite case, fitness is properly represented as a deterministic function, defining the *expected reproductive success*. It is a deterministic component in a stochastic model. Assuming that, in finite cases, fitness must be probabilistic risks conflating the effects of selection with those of drift, and collapses the distinction between expected and realized fitness. Fitness values tell us what the *expected* values are, even though we know that, in finite populations, drift, rounding error, and the like will disperse *actual* values around the mean this provides. Alternatively, the fitness of a phenotype becomes the mean value in a sufficiently large population. In any finite population, or any finite set of populations, even the average of the realized fitnesses will deviate from what would be expected if fitness were the only determinant of evolutionary change. Similar consequences follow when environmental heterogeneity induces variance: environmental variance results in fitness across the ranges of environments being a probabilistic distribution.

3. Why Propensities Rather than Limiting Frequencies?

Defenders of propensity interpretations offer a variety of reasons for treating the probabilities involved as propensities. Having dismissed the interpretation of fitnesses as actual frequencies, there are two options: fitnesses can be identified with objective propensities or with limiting frequencies. One standard interpretation of probability depends on the frequencies in the “long run” (Hacking 1965, ch. 4). For our purposes, it does not matter whether the “long run” is infinite or not, so long as it is effectively infinite. Given an environment or a distribution of environments, the limiting frequen-

cy of a genotype or phenotype is the frequency that will occur if the sequence is continued over the “long run”. The question is whether, assuming a probabilistic interpretation of fitness, these probabilities should be interpreted as propensities rather than as limiting frequencies or frequencies in the “long run”. Alternately, the question is whether, within a probabilistic framework, fitness should be interpreted as providing the likely expected values rather than the values expected in the “long run”.

The problem is that limiting or “long run” frequencies are not always well defined; whether they are depends on whether the frequency in question “settles down” to a stable limit. As is now commonplace from the work of May (1972, 1973) and others, for some biologically plausible parameters, we encounter periodic oscillations in frequency—that is, limit cycles—or chaotic variation in relative frequency, destabilizing the system until it “crashes”. Additionally, there are biologically plausible cases in which there are stable limiting frequencies whose value depends on the actual sequence of environments. Such is the case, for example, when two competing types are at or near an unstable equilibrium such that whether one or the other predominates depends on the actual sequence of environments; for example, one or the other may predominate depending on whether a series of relatively dry or relatively wet seasons occurs first. This is one aspect of the notorious role of historical accident in evolution. Lewontin (1985) holds that such sequence dependence is common in evolution. Cohen (1976) has shown that a number of biologically realistic cases can be simulated by sampling with replacement; this means that, again with reasonable parameter values, each run has a stable limit even though the limits of a series of runs are randomly dispersed. There is no unique and well defined limit in such cases. The risks of sequence dependence and of the non-existence of the relevant limits faced by “long run” interpretations of the probabilities show that they are in principle unsuited for defining fitness because they yield mistaken values.

The point is that attempts to provide a probabilistic definition of fitness by use of “long run” frequencies will often yield mistaken values, or no univocal value, for the relevant probabilities. They will yield no value whatsoever where there are limit cycles or chaotic regimes. They will yield no univocal value in cases of sequence dependence. Yet, fitnesses are generally regarded as well defined in such cases. We think they *are* well defined. So much the worse for this class of attempts to define fitness.

It is, perhaps, worth remarking on one way in which one might attempt to employ limiting or “long run” frequencies counterfactually to define or evaluate fitnesses. Some of the problems we have discussed depend in important ways on environmental variation. Since fitness is relativized to environment, it might appear that these problems are simply irrelevant. We might fix the environment exactly as it currently is—for example, by holding the relative number of competing organisms constant, or by fixing the range of temperature and rainfall excursions—and then evaluate the “long run” frequencies within these fixed regimes.⁹ In fixing the biotic environment we exclude all forms of frequency dependent selection and limit cycle phenomena; similarly, in fixing the abiotic environment, we exclude interactions between organism and environment that in fact play a role in evolutionary dynamics. The most significant problem here is the systematic underestimation of the importance of variation in biotic interactions from one generation to the next. This introduces feedback relations which are crucial in assessing fitness. As Richard Levins and Richard Lewontin comment,

The simple view that the external environment changes by some dynamic of its own and is tracked by the organisms takes no account of the effect organisms have on the environment. The activity of all living forms transforms the external world in ways that both promote and inhibit the life of organisms. (1985, p. 69)

For organisms, most strikingly in small populations, variation in population size from generation to generation by itself represents *variation in biotic environments* that may significantly affect fitnesses. The same may be said for changes in the relative frequency of alternative phenotypes (Maynard Smith 1982). Fixing the environment, whether biotic or abiotic, in calculating fitnesses is biologically unrealistic, and badly distorts the notion of fitness that is to be explicated. One can obtain stable long run frequencies by requiring a stable environment, but only at the expense of a realistic account of fitness. This maneuver cannot save an interpretation of fitness that depends on frequencies over the “long run”.

4. Which Propensities?

Beatty and Finsen (1989) raise a number of difficulties for propensity interpretations of fitness. Some of their concerns seem to be mistaken. The central difference between their position and ours turns on the recognition that fitness is a relation between an entity in an evolving lineage (for example, an organism) and *its* environment. Specifically, we think it is important to insist on a careful analysis of *which* environments are relevant to an organism in assessing its fitness. This underscores questions of scale. Our analysis eliminates many of the propensities that Beatty and Finsen consider to be relevant measures of fitness, though more than enough remain as contenders.

The importance of issues of scale arise, for example, in Beatty and Finsen's claim that among the many propensities that might measure the fitness of a (type of) organism are the “expected time to extinction” (ETE). They (1989, pp. 20-1 and 26-7) also consider the use of long term effects as the relevant measure of fitness, evaluating these, for example, by reference to the relative numbers of distant progeny. Our assessment of the mutual relevance of long and short term fitnesses turns crucially on the issue of scale. Differential multiplication of organisms alters the selective environment (cf. Brandon 1990; Antonovics, et al., 1988); accordingly, long term *extrapolations* on the basis of current fitnesses are not appropriate measures of *current* fitnesses. Moreover, increases in fitness can trap lineages in evolutionary dead ends. Such traps are sometimes predictable. Rather than demonstrating that the resultant low long-term fitness makes the choice of an appropriate measure of current fitness more difficult, however, this argument shows the irrelevance of ETE and of expectations about long term fitness as measures of the fitness of *organisms*. It may be that ETE is an appropriate measure of the fitness (or a component of the fitness) of higher level taxonomic units such as species or genera (cf. German 1991; Sepkoski 1991). It cannot provide an appropriate definition or estimate of fitness at the organismic level, and therefore does not provide a useful *general* definition of fitness. Fitness is a measure of the relations of a unit to (expectable) *current* environments. Indeed, this is precisely what fitness must be for it to be *contingently* related to long-term evolutionary outcomes. Long-term survivorship propensities, even if well defined and calculable, are not fitnesses.¹⁰

It is important to recognize the fundamental move in the preceding argument. For a vast number of biological situations, the salient aspects of the selective environment are biotic. In cases of frequency dependence, for example, a new generation typically faces a different selective regime from preceding generations. Thus, proper delimitation of the biotic aspects of the selective environment is crucial to any measure of fitness. Since the biotic and abiotic environments exhibit significant change (cf. van Valen's 1973 red queen hypothesis), in the vast preponderance of biologically realistic cases any sound measure of fitness is restricted to the current range of (expectable) environments. This refocuses the difficulties in achieving propensity accounts of fitness to the problem of delimiting the appropriate range of current or currently expectable environments with which the organism (or, generalizing, the unit of evolution) must interact.

These considerations suggest a principle in assessing what constitutes a relevant environment, and the relevance of “long-term” considerations to fitness. In cases in which an organism (say, an insect with a two-week generation time) employs environmental cues to make facultative adjustments to long-term (say, seasonal) cycles, the interrelation between the organism and the environment justifies the inclusion of the range of environmental excursions over *that* particular length of time in evaluating *current* fitness. Where there is no such ‘informational feedback’ between environmental changes and the properties of the organism, the long-term considerations are not appropriate in evaluating current fitness. We do not exclude dynamic patterns, but insist that one be sensitive to matters of scale.

The notion of ‘informational feedback’ provides the basis of an account of relevance. It also accounts for cases where fitnesses are assessed across two or more generations. One example is Fisher’s (1930) well-known argument explaining the rough equality of the sex ratio in most sexual species: to maximize representation in the F_2 generation, it pays to produce minority sex offspring in the F_1 generation. What is crucial to the assessment of relevance here is the informational feedback rather than the physical details on which it supervenes; the organism systematically abstracts from these physical details in fixing on features that it uses as cues. To assess the putative relevance of environmental features to selection and fitness, one must ascertain whether there is a feedback at the appropriate level. Where no environmental information is available about the relevant features of the environments of, for example, the distant future one can exclude long term measures of fitness. This provides the proper content for the metaphor of ‘blind evolution’.

These points do not remove all the difficulties that Beatty and Finsen raise for the refinement of propensity definitions or measures of fitness. In particular, we offer no solution here to the problems posed by the fact that in very similar circumstances distinct statistical measures (sometimes variances, sometimes means, etc.) correlate with the expected contribution to the next generation of organisms or other units. As Beatty and Finsen show, such problems arise naturally when organisms (units of evolution) can produce varying numbers of offspring (descendant units) with some sort of probability distribution.¹¹ But though we have not handled *these* problems, our argument helps to separate difficulties which are important from those that are spurious.

To summarize, the best interpretations of fitness as a propensity make fitness a *causal consequence* of the features of an organism in a relevant range or distribution of (expectable) environments. The most sensitive issue that this leaves open is the delimitation of the relevant environments and the interpretation of relevance. Fitness for an organism is then a matter of the likely number or distribution of offspring given the relevant environments. Because organisms are members of potentially continuing lineages, fitness can predict evolutionary outcomes, although it is a weaker and more fragile indicator than many optimistic selectionists have believed.

5. Conclusion and Prospects

We have focussed mainly on issues regarding the concept of fitness in evolutionary theory, but our position has larger implications. Since fitnesses are measures of evolutionarily relevant interactions between organism and environment and since fitnesses cannot be analyzed solely in terms of the mechanistic underpinnings on which they depend, various versions of reductionism are misguided. In particular, we reject the consequences that Rosenberg, for one, draws from supervenience:

... everything that the theory of natural selection can explain about what is happening in a well-controlled laboratory experiment can be explained more deeply, more directly, and in greater detail by physiological and biochemical principles that *do not mention the supervenient evolutionary concept of fitness*. When enough theoretical and experimental detail has been gathered to make a prediction that specifically confirms the claims of evolution about the maximization of fitness, the theory of natural selection and the notion of fitness become *superfluous*: ... The prediction that can be extracted from [evolutionary] theory in such cases is at best generic, and the explanation it provides will be qualitative at most. (Rosenberg 1985, pp. 173-4, his emphases)

We need not dispute the reality of supervenience; however, an account restricted to the “vast and heterogeneous class of determinants of fitness” fails to capture the patterns and processes which evolutionary theory aims to explain. It is simply false that what is explained by fitness can be explained by “physiological and biochemical principles”. For example, a 50:50 sex ratio in peas might be explained by cytological mechanisms, but it may require shifting to an evolutionary model such as Fisher’s to explain the general prevalence of 50:50 sex ratios. The patterns and processes which are the core of evolutionary theorizing are intelligible only at a higher level of abstraction. The physical principles themselves provide an inadequate account of causal relevance. What supervenes on physical differences will be the actual, realized, fitness, and there will be a systematic difference between fitness understood as a propensity—that is, fitness as it is employed in evolutionary theory—and the values resulting from physical differences. Indeed, in any given finite population, even if the expected mean value for an evolving trait is a deterministic function of prior values, given selection and heritable variance, the *actual* mean value is more likely to deviate from the expected value than not, and the actual value is what will be determined by the physical “determinants of fitness”. Expected fitness is indispensable, and cannot be defined in terms of the actual values achieved. An account which emphasizes supervenience fails to respect the distinction between expected and realized fitness. Of course, we could always pick out some subset of the phenotypic and genotypic properties which would yield appropriate fitness values, but there is no principled means, absent an account of the selective regime, for reading out the correct subset of physical characters from the “physical and biochemical principles” on which fitness is supposed to supervene. Not all the physical features of the organism or its environment are relevant to evolutionary processes or patterns, and the “physical and biochemical principles” on which fitness supposedly supervenes cannot tell us *which* features matter for evolutionary processes and patterns. Selection operates at a level between the chaos of detailed interactions particular to each organism and one that ignores the complexities of environmental variation and biotic interaction. The relevant selective environment, or range of expectable environments, is that in which there is informational feedback between the organism and the environment, both biotic and abiotic. This cannot be given a purely physical analysis.

Notes

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edge this support. We have benefitted from discussions with Janis Antonovics, John Beatty, Robert Brandon, Greg Cooper, Rebecca German, Donald Gustafson, Brent Mischler, W. E. Morris, and Kelly Smith.

²Unless otherwise specified, we use *fitness* to mean *expected fitness* as opposed to *realized fitness*. Brandon (1990) calls expected fitness *adaptedness*, distinguishing it from fitness. The significance of the distinction is the same.

³It is another matter, and equally important, to be able to discriminate the effects of drift and selection empirically. This turns out to be a difficult matter for a number of reasons, though it is one that can be done in some cases. It is clear in any case, that if the effects of selection and drift are collapsed and cannot be distinguished conceptually, any empirical discrimination would be impossible.

⁴There are a number of possible sources of stochastic effects that are not central for our discussion. If, for example, heritability is not perfect then developmental noise may change the distribution from what would be predicted on the basis of fitness differences alone. This clearly does not imply that fitness is itself a probabilistic quantity. Similarly, in finite populations there will be effects of averaging from theoretical selection values comparable to rounding error. Such effects are not stochastic; they do not support the claim that fitness *per se* is a probabilistic function.

⁵We trust that Rosenberg intends to include encounters with other organisms under "interaction with physical properties of the environment." A great deal turns on the way in which biotic interactions enter into fitness functions; such formulations as Rosenberg's underemphasize their importance.

⁶As Brandon has reminded us, drift will change the variance and also the mean within finite sets of populations. This is easily seen, since a finite set of finite populations will be a finite population, and thus subject to some sampling error.

⁷Even in the purely stochastic (neutral) case where there is no selection, the mean value of the ensemble would not be expected to change, despite the fact that there will eventually be no populations that are polymorphic.

⁸There are more realistic models incorporating density dependence, but that does not affect our central point.

⁹Brandon suggests averaging across environments. This would have the same effect.

¹⁰There is a difficulty regarding the characterization of 'long-term' here; consider the case of annual seasonal cycles in the case of short-lived organisms that adopt different morphs or switch from asexual to sexual reproduction on a seasonal basis.

¹¹Roughly the problem is that the relative contributions of different organisms in a given distribution of expectable environments depends, in various circumstances, on the *variance* of the expected distribution of offspring number and on other statistical differences between them even when the *mean* number of expected offspring is identical as between the types (cf. Lacey, et al., 1983). We view this as a problem concerning the appropriate *measure* of fitness, not its *definition*.

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