Fitness As a Function[1]

Henry Byerly

University of Arizona

Recent attempts to clarify the fitness in evolutionary theory as a propensity (Brandon 1978; Brandon and Beatty 1984; Burian 1983; Mills and Beatty 1979; Sober 1984a, 1984b) or as a primitive theoretical term (Rosenberg 1983, 1985; Williams 1970, Williams and Rosenberg 1985) all miss the mark in clarifying the empirical content and explanatory power of natural selection theory.

I shall argue that the crucial distinction missing in these accounts is between the sense of fitness common in population genetics as actual relative rate of increase of genotypes and fitness in the more ordinary sense--and Darwin's--of adaptedness of organisms. The relation between these senses of 'fitness' is that fitness as actual reproduction success depends on, is a function of, variables representing adaptive capacities and environmental properties. I shall show how failure to honor this distinction has greatly confused a number of already complex issues concerning the theory of natural selection.

1. Fitness and Adaptedness

The process of natural selection consists in changes in the relative numbers of different genotypes in a population. Evolutionary theory seeks to explain these changes by showing their dependence on adaptive characteristics of organisms interacting with environmental variables under constraints of genetic transmission processes. The dynamics of natural selection can be represented schematically by exhibiting the rate of increase f_i of a genotype *i* as a function of adaptive properties of the organisms and environmental variables:

$$f_i = (dN_i/dt)/N_i = F(N_i, A_i, E),$$

where N_i is the population size, A_i represents various properties of organisms (e.g. birth rate b_i and death rate d_i), and E represents environmental variables. (See Bernstein *et al.* 1983 for a discussion of such a representation of the dynamics of natural selection). I shall not try to deal with questions of how to fill out such a schema, theoretically or practically, except to examine conceptual problems

PSA 1986, Volume 1, pp. 494-501

https://doi.org/10.1086/psaprocbienmeetp.1986.1.193149

posed by such a formulation of the dynamics of selection, in particular the very notion of intrinsic adaptive properties of organisms. I shall call fitness as relative rate of increase of a genotype F-fitness (after Fisher); fitness as representing the totality of intrinsic adaptive properties of organisms is designated A-fitness (adaptedness); and fitness on the propensity interpretation is P-fitness.

The charge has repeatedly been made that that natural selection, as an explanation for evolutionary change, is empirically empty, since the principle of natural selection as Darwin expressed it in the notorious phrase "survival of the fittest" is tautological. If 'fittest' means simply surviving in greatest numbers, the principle seems to say only that those organisms which survive, survive. What Darwin plausibly intended to assert was rather the evolutionary success of the more adapted. Survival means increased representation in future generations; fitness means the best adapted. A-fitness leads to F-fitness. (This interpretation is suggested in Bernstein *et al.* 1983 and a similar one in Burian 1983.) This distinction will aid in clarifying the remarkably complex tangle of conceptual issues concerning the concept of fitness and the natural selection process.

2. The Propensity Interpretation

The propensity interpretation of 'fitness' was motivated in large part as an answer to charges of circularity in explaining actual differential reproductive success (F-fitness) of different kinds of organisms by their differential fitness. The concept of fitness that is supposed to explain reproductive success is defined not as actual reproductive success but as a probabilistic disposition or propensity for reproductive success. P-fitness, the propensity interpretation, is related to F-fitness, defined in terms of numbers of actual offspring, as soluble is related to dissolving. Then Darwin's principle of natural selection is supposed to take on empirical content in the sense that "the soluble (substance) is dissolving" is empirical (Mills and Beatty 1979, p. 270n). One problem with this move is that even if not analytic, a propensity to dissolve hardly explains dissolving in any interesting sense--at best it points to an explanation. But another problem for the propensity interpretation is that we want a concept of fitness that can be used to explain evolutionary change. This is F-fitness. The actual relative rates of increase of different genotypes over time determine the genetic basis for evolutionary change of kinds of organisms and their adaptations.

A touchstone case for analysis of the concept of fitness which the propensity interpretation is designed to resolve is a set of identical twins who developed in the same environment but have different numbers of offspring. Do they differ in fitness? If the fitness of an organism is simply the number of offspring actually produced, then the fitness of one identical twin who has many offspring could be high and that of her twin with no offspring zero. But this seems to violate our notion of what "fitness" should mean. The propensity interpretation resolves this question by appealing to the probabilistic nature of the selection process. The twins differ in actual reproductive success but have the same expected values of reproductive success, that is, the same P-fitness.

The problem is actually rather complex when examined more closely. If the twins have the same genotype, the actual difference in number of offspring must be caused by some environmental differences which include environmental effects on development (assuming there is no "pure chance" in the sense of quantum physics operating). There are several strands to this question which need to be sorted out.

(1) One reason it sounds odd to say that the fitness of an organism with zero offspring is zero is that 'fitness' in ordinary usage tends to mean the same as 'adaptedness'. The twin with zero offspring might be quite viable and fit in her environment.

(2) F-Fitness, as I define it, applies to genotypes and only derivatively, as per capita rate of increase, to individual organisms. Thus each individual having a certain genotype *i* has the same F-fitness. Each twin has the same F-fitness.

(3) The difference in environment responsible for the difference in number of offspring distinction is "accidental" with respect to systematic causes of F-fitness. Causes affecting organisms are accidents if they are random with respect to differences in genotypes being selected, and thus not relevant to evolution *by natural selection*. If by chance all organisms with genotype *i* are eliminated, the *j* genotype survive to go on to reproduce and predominate in a species, has there been natural selection for genotype *i*? Sober (1984) would say: there is natural selection *of* the organisms corresponding to *j* but not *for* the *j* phenotype.

(4) The twin example can also be used to raise questions concerning a distinction of intrinsic versus relational properties. What is required for the twins to have the same A-fitness (intrinsic adaptedness)? Can sense be made of intrinsic adaptive properties of organisms? Surely if two organisms have the same genotype, and thus the same A-fitness (and even if they develop the same phenotype), they can different greatly in F-fitness, which is also a function of environmental variables. This question will be considered below.

Brandon, unlike most philosophers discussing fitness, distinguishes between adaptedness and fitness. He remarks, fittingly, that lexical parsimony is out of place here, that "one shouldn't cloud the issue [of the relation between fitness and adaptedness] by using one word for two separate but closely related and easily conflated concepts" (1981, p. 429). He uses 'fitness' in the sense of F-fitness (ironically often called Darwinian fitness) with one difference: I defined F-fitness at the genotype level. But Brandon's concept of adaptedness is just P-fitness. He defines relative adaptedness of an organism in environment E as an expected value of the number of offspring. He wants, like others proposing a propensity interpretation, to claim nontrivially that adaptedness explains differential reproduction. His principle of natural selection states that organisms better adapted to their environment tend to have greater reproductive success: Probably [If a is better adapted than b to their mutual environment E, then a will have greater reproductive success than b (in E)] (1981, p. 428). Brandon acknowledges that his principle of natural selection has "no biological empirical content" but "is simply an application of probability theory to a biological problem." (p. 432) He claims, however, that instantiations of the principle do have empirical biological content. He achieves this by shifting the sense of "adapted": He "cashes out" adaptedness (P-fitness) by providing a causal basis for adaptedness. But causes of fitness differences (e.g. adaptive color differences of melanic moths) are not simply instantiations of differences in adaptedness in his sense. All we get directly as an instantiation is that if some particular moth *a* has higher expected number of offspring than *b*, then *a* will have greater reproductive success than *b*.

The propensity interpretation of fitness misplaces the operative propensities and runs together the contrast of actual versus potential with deterministic versus probabilistic. The fitness values which determine evolutionary change in a population are the actual values, not expected values. The dynamics of the selection process proceed whatever the causes of the actual values. What needs to be clarified is the division of the actual process of selection into components due to systematic relations between adaptive characteristics and environmental variables and stochastic factors. Conflating realized with expected fitness (Burian 1983, p. 302) is not the major problem in the tautology charge. This touches only the chanciness of the functional dependence of actual reproductive success on adaptational and environmental variables. This contrast does raise the important question of the role of chance in evolution, for example, the role of genetic draft, but the basic tautology problem would be essentially unchanged if the actual number of offspring were fixed deterministically for a given genotype in a given environment.

3. Relational and Intrinsic Properties

It is common to insist that fitness is a relational concept. For example, Rosenberg emphasizes that "fitness is a relational property, reflecting the interaction of an organism and its environment." (1985, p. 155). The point is that fitness (actual reproductive success) *depends* on environmental variables rather than simply on properties of the organism. The rate of increase of genotypes is a function of environmental as well as intrinsic property variables. The original sense of 'fitness' is like a key fitting a lock. The shape of the key, an intrinsic property of the key, fits the shape of the lock. The fitness here is a relation between shapes. There is, however, no simple property of organisms analogous to shape which corresponds to the sum of the contribution of adaptive characteristics of organisms to fitness.

If adaptedness is taken to be the total propensity of genotypes-in-an-environment, that is, as P-fitness, then adaptedness is not a property of the organism but a relation between an organism and its environment. Confusion results from assimilating adaptive properties of organisms, first to a global adaptiveness, viewed as a disposition, and then making adaptive properties of organisms "relational" by fusing adaptive properties of organisms with environmental properties as a propensity to have F-fitness. Such a fitness propensity, which represents the sum of determining conditions of relevant properties of organisms and environmental variables, plays no role in evolutionary theory. Evolutionary theory would be much simpler if we could define a significant sense of overall adaptedness of a genotype as the sum of the intrinsic adaptive characteristics. But no such tractable property has been forthcoming. Though no global property of adaptedness, with criteria independent of F fitness, is available there are general components of adaptedness: intrinsic birth rate, death rate, resource utilization which are more tractable and particular phenotypic traits, which though not so directly related to a functional determination of fitness inject empirical causal content into the dynamics of natural selection.

There are serious questions about the sense in which we can isolate intrinsic adaptive properties such as an intrinsic birth rate b_i of which F-fitness is a function. Is b_i really a further function of environmental variables? Intrinsic birth rate contrasts with actually manifested birth rate. Actual birth rate depends on both the genotype of the organism and its environment. Suppose that the actual birth rate (for a range of genotypes of a species) depends on temperature in a certain way. We might try to abstract an intrinsic capacity at temperature T_0 and then formulate some "nice" function for temperatures around this range. Two questions need to be disentangled here:

(1) What is the contribution of the genotype i which gives rise to a particular birth rate b_i in different environmental circumstances?

(2) Does there exist a relatively simply function for fitness dependence on b_i that is common to different genotypes i and j?

There seems to be no continuity of structural changes in genotype with changes in intrinsic birth rate since a slight change in genotype (a point mutation) might lead to sterilty and zero birth rate. But for a given genotype, the genotypic contribution can in principle be abstracted from the relational consequence of actual birth rate.

4. Causes and Effects

What serves to cause and explain actual reproductive success in the relevant way in evolutionary theory is not fitness as a propensity but the variables of which Darwinian fitness is a function. Rosenberg says that "fitness must be measured by its effects" (1985, p. 156), and the relevant effect is F-fitness: "the fitness of an organism is measured by counting progeny" (p. 157). Of course, F-fitness is not measured by its effects but by what it is: relative rate of increase. We might say that adaptedness is measured by or revealed operationally by its effects on F-fitness. F-fitness is a function of adaptive characteristics (along with environmental variables) and the effects of F-fitness are evolutionary changes.

It is difficult to interpret just what Rosenberg does mean by his 'fitness'. He wants a concept of 'fitness' which is freed from reproduction rates. His fitness is not F-fitness, but he also rejects P-fitness as an otiose concept in the theory of natural selection. The P-fitness disposition has, he contends, no "manageably specifiable base in occurrent properties" (1985, p. 163). Yet he seems to mean something like P-fitness. What can he mean when he says that adaptive characteristics of organisms cause "fitness" which in turn causes F-fitness?

It is no wonder that he, agreeing with M. Williams, concludes that the way out of problems about defining 'fitness' is to take it as a primitive term in evolutionary theory. Construing 'fitness' as a primitive term, undefined in the theory, appears to make a deft cut through knotty conceptual problems. F-fitness is, of course, defined for the theory (in the same sense as 'acceleration' for Newtonian mechanics or 'work' for thermodynamics). Adaptedness is not defined within the theory of natural selection (certainly not in Williams' formalization), but as P-fitness it plays no role in the theory. Nothing like Rosenberg's global supervenient concept of fitness as that which causes F-fitness plays a role in evolutionary explanations. (Even if there were such a concept in evolutionary theory, there are difficulties with the notion that a theory delimits or "implicitly defines" its primitive terms, but I will not explore this question here).

Why are the two concepts fitness and adaptedness needed to explicate the theory of natural selection? Values of F-fitness govern the dynamics of the selection process. We want to abstract the intrinsic adaptiveness of the organism, its design, from the sum of the organism-environment interactions which is the propensity for actual reproductive success since it is a goal of the theory of natural selection to explain the adaptive properties of organisms. We explain the evolution of the design of organisms in terms of the contribution of the intrinsic design properties to F-fitness. The solubility analogy can be helpful here. Solubility, as a property of a substance (say water solubility of sugar) is not relational. Dissolving is a relation between the sugar and the water. Dissolving is a function of intrinsic capacities of the sugar (which drives back to molecular structure) and conditions of the water. Making F-fitness a function of adaptive capacities and environmental conditions is like making the dissolving of a lump of sugar dependent on, a function of, the molecular structure of the sugar and such conditions as contact with water at a certain temperature.

Actual reproductive success, F-fitness, is a relation between organisms and the environment. To express this relation as a function, we need to relate variables measuring adaptive properties of the organism to environmental variables. We do not want the adaptive properties to be in turn relations between the organism and its environment. This would threaten the kind of problem Russell and Moore saw for absolute idealists: if to know the reference of the relata 'a' and 'b' of a relation Rab we must first understand the relation Rab, how can we state the relation as holding between definite entities? What is the 'it' in a claim that it, intrinsic birth rate say, would not be what it is apart from its relation to the environment?

It is right to emphasize the role of "engineering fitness" (adaptive causes of rate of increase), (Burian 1983), but this does not mean that realized fitness, F-fitness, does not play a role in evolution. Indeed, in abbreviated form we can say: adaptive characteristics explain (causally contribute to) rate of increase of a genotype. Relative rate of increase of genotypes explains--results in over time--evolution (change of gene frequency). Abbreviating, and taking 'fitness' in the sense commonly employed in evolutionary theory: adaptations cause, explain fitness; and fitness causes, explains adaptations. In consequential functional explanation, adaptations appear to cause their own existence (that is, to be less paradoxical, effects of adaptive traits cause the existence of those kind of traits in the selection process). If there really were an overall design in evolution, we might say not only that fitness is a (mathematical) function of adaptations but also that adaptations are a function of fitness. Of course, it is part of Darwinian paradigm that the natural selection process itself has no "function"--it causes design but is not itself caused by design.

Why has the distinction suggested between fitness as rate of increase and adaptedness been commonly rejected or misconstrued? One reason is the special conceptual difficulties which "adaptedness" raises. The concept of adaptedness, as distinct from F-fitness, is what makes evolutionary theory so different from other theories. (Perhaps there is some analogy to difficulties in relating our concept of disorder to the technical concept of entropy.) Population geneticists, when focusing on problems of calculating the effects over time of fitness values (selection coefficients), can conveniently ignore questions about adaptive value and functional explanations. The virtue of marking a distinction between F-fitness and adaptedness is not that simply by avoiding ambiguity we can easily resolve questions about how natural selection operates. The importance of distinguishing between fitness and adaptedness is that this allows questions, which might otherwise be passed by, to stand forth with greater clarity.

Notes

[1] I wish to thank Harris Bernstein, Fred Hopf, Evelyn Keller and Richard Michod for helpful discussions.

References

Bernstein, Harris; Byerly, Henry C.; Hopf, Frederick A.; Michod, Richard A.; and Vemulapalli, G. Krishna. (1983). "The Darwinian Dynamic." Quarterly Review of Biology 58: 185-207.

Brandon, R. (1978). "Adaptation and Evolutionary Theory." Studies in History and Philosophy of Science 9: 181-206.

----------. (1981). "A Structural Description of Evolutionary Theory." In PSA 1980. Volume 2. Edited by P.D. Asquith and R.N. Giere. East Lansing, Michigan: Philosophy of Science Association. Pages 427-439.

----------- and Beatty, J. (1984). "The Propensity Interpretation of 'Fitness'--No Interpretation Is No Substitute." Philosophy of Science 51: 342-347.

Burian, R. (1983). "Adaptation." In Dimensions of Darwinism. Edited by M. Grene. Cambridge: Cambridge University Press. Pages 287-314.

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

Rosenberg, A. (1983). "Fitness." Journal of Philosophy 80: 457-473.

------------. (1985). The Structure of Biological Science. Cambridge: Cambridge University Press.

Sober, E. (1984a). The Nature of Selection. Cambridge, MA: MIT Press.

--------. (1984b). "Fact, Fiction and Fitness." Journal of Philosophy 81: 372-383.

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

-------------- and Rosenberg, A. (1985). "'Fitness' in Fact and Fiction: A Rejoinder to Sober." Journal of Philosophy 82: 738-749.