

KEYWORDS IN EVOLUTIONARY BIOLOGY

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FITNESS: HISTORICAL PERSPECTIVES

Diane Paul

"FITNESS" is perhaps the most contentious concept in evolutionary biology. How did the word enter the vocabulary of evolutionary biology, and how has its meaning changed over time?

Charles Darwin employed the verb "fit" synonymously with "adapt," and the adjective "fitted" with "adapted" or "suitable." The noun "fitness" appears only once in the first edition of *On the Origin of Species*: "Nor ought we marvel if all the contrivances in nature be not, as far as we can judge, absolutely perfect; and if some of them be abhorrent to our idea of fitness" (1859b, p. 472). But Darwin did, of course, ultimately use the expression "survival of the fittest," and this is the route through which the noun came into common use in biology. The actual phrase "survival of the fittest" first appeared in Herbert Spencer's *Principles of Biology* (1864), where it was employed simply as a synonym for Darwin's term "natural selection."

Notwithstanding his socialist sympathies, Alfred Russel Wallace was a great admirer of Herbert Spencer. Wallace was also concerned at the many misunderstandings that had arisen among Darwin's readers from the assumption that selection requires conscious thought and direction—that is, a selector. In 1866 he wrote to Darwin, arguing that much needless confusion had resulted from Darwin's choice of "natural selection" as well as his constant personification of nature as "selecting," "preferring," and so forth. In Wallace's view, "survival of the fittest" would both describe the theory more accurately and also avoid the misunderstandings that had plagued it from the beginning. As early as 1860 these difficulties had led Darwin to assert that, were he to start over, it would be with a different term. By 1866, however, he was reluctant to abandon "natural selection." He eventually agreed to compromise; although he would not give up his own phrase, he would work Spencer's into the *Variation of Plants and*

Animals under Domestication (1868) and the fifth edition of the *Origin* (1869). In his succeeding works, the terms are used interchangeably.

Darwin did not believe that he was taking a significant step in describing his theory as the "survival of the fittest." Fitness and its various cognates, however, had ordinary-language meanings that colored the ways in which it was read. In Victorian Britain and the post-Civil War United States, "survival of the fittest" came quickly to imply that the socially successful deserved the rewards of their position. To interfere with the status quo was to reverse the process of natural selection and thus ensure, in the words of the economist and sociologist William Graham Sumner, the "survival of the unfittest." And the unfit were already doing quite well; indeed, they appeared to be rapidly out-breeding their betters. "If the fittest do not serve as parents, the next generation will not inherit fitness" warned the biologist and eugenicist David Starr Jordan (1911, "Prefatory Note"). Thus it seemed necessary to adopt policies designed to increase the birth rate of the more prosperous groups and to limit that of the less prosperous. The "survival of the fittest" was invoked to support policies of economic laissez-faire and of reproductive intervention.

The development of population genetics in the 1920s and 1930s undermined the colloquial usage of fitness in evolutionary biology. In the work of J. B. S. Haldane, Sewall Wright, and R. A. Fisher, the gene was identified as the target of selection and selection itself was redefined as a change in gene frequencies. The measure of fitness became success in producing offspring, irrespective of the causes of that success. Moreover, what began as an indicator of fitness soon came to define its meaning. Haldane gave this new concept the (somewhat improbable) tag "Darwinian fitness" in his book *The Causes of Evolution* (1932).

During the 1930s and 1940s both old and new meanings of fitness coexisted. Thus Haldane himself could write that modern war destroys "the fittest members of both sides engaged in it," when it served his social purposes (1937b, p. 151). By the 1950s, however, biologists no longer employed the word in its vernacular sense, even in their popular writings. The growth of population genetics had played an important role in this development but so also had political events. With the rise of Nazism, evolutionary biologists outside of Germany struggled to disassociate their science from racial and class prejudice. Some tried to replace fitness with phrases whose past was less problematic, such as "adaptive value"; these efforts met with limited success. At the same time, politically liberal or leftist biologists such as Theodosius Dobzhansky, I. Michael Lerner, L. C. Dunn, and C. H. Waddington vigorously emphasized the concept's value-neutrality. A passage from the textbook *Principles of Genetics* by E. Sinnott, Dunn, and Dobzhansky illustrates the relationship between

some biologists' social concerns and their insistence that fitness *is* reproductive success. After noting that nineteenth-century evolutionists had equated natural selection with a "struggle for existence" leading to the "survival of the fittest," the authors write: "These emotionally loaded phrases have been often misused for political propaganda purposes. A less spectacular but more accurate statement is that carriers of different genotypes transmit their genes to the succeeding generations at different rates . . . The 'fittest' is nothing more remarkable than the producer of the greatest number of children and grandchildren" (Sinnott et al., 1958, pp. 100–101).

In attempting to solve one problem, however, they had created another. If fitness is defined as success in surviving and reproducing, the statement that the fittest survive is apparently emptied of content. Thus was born the famous "tautology problem," which has bedeviled the field ever since.

FITNESS: THEORETICAL CONTEXTS

John Beatty

THE PRECISE meaning of "fitness" has yet to be settled, in spite of the fact—or perhaps because of the fact—that the term is so central to evolutionary thought. After all, evolutionary theory itself is still in flux.

An acceptable definition of the term "fitness" must be consistent with the role played by that term in evolutionary explanations. However fitness is defined, it must at the very least be positively correlated with evolutionary success, or in other words, with representation in future generations, for this is what higher fitness is invoked to explain.

One simple and apparently straightforward way of sustaining the connection between fitness and evolutionary success is by defining "fitness" as actual offspring contribution (see, e.g., Crow and Kimura, 1970, p. 5; Dobzhansky, 1975, pp. 101–104; see also Endler, 1986, pp. 27–51, for a discussion of a variety of different notions of fitness). But this construal has what are, to many, unappealingly counterintuitive consequences. Take the widely cited case of the identical twins, one of whom is, by chance, killed by lightning prior to its first reproductive encounter, the other of whom happens not to be in the path of the lightning and lives to contribute many offspring to the next generation (Scriven, 1959). Must we attribute different fitnesses to these otherwise indistinguishable twins?

One might suggest that the counterexample loses its force when the conception of fitness in question is suitably relativized. Fitness is offspring contribution *in a particular environment*. An organism that is highly fit in one type of environment—say, a strong and cunning lion in a savannah full of zebras—may be unfit in a different environment—say, a savannah full of lion hunters. Similarly, our imaginary identical twins have the same fitness only *in the same environment*, not when one is subjected to high voltage while the other is spared. The counterexample, it might be argued, does not apply to the twins' situation.

Yet in an important sense the twins do share the same environment, one in which the chance of an encounter with lightning is rare. The counterexample cannot be so easily circumvented.

One reason it seems so counterintuitive to suggest that the twins' different offspring contributions reflect differences in their fitness is that their different offspring contributions seem instead to be a matter of "chance." Indeed, evolutionary biologists distinguish those cases in which differential evolutionary success reflects differences in fitness and those cases in which it does not; the latter sort of case they refer to as evolution by "random drift."

The problem with the interpretation of fitness as actual offspring contribution is that it does not sustain this distinction. More specifically, the problem with the interpretation of fitness as actual offspring contribution is that it is not sufficiently probabilistic, because in order for the distinction in question to be sustained, there must be some chance that two organisms with the same fitness can leave different numbers of offspring. Interestingly, Darwin himself always wrote of those organisms that have the "best chance" of surviving and reproducing (see, e.g., Darwin, 1859b, pp. 61, 81).

Perhaps the simplest way of patching up the conception of fitness as actual offspring contribution is to construe fitness as the *average* number of offspring of a *type* of organism. Among organisms of a particular highly fit type, some will, by chance, do better, and some will, by chance, do worse, but the type as a whole will leave a relatively high number of offspring on average (this is a common conception; see, e.g., Emmel, 1973, p. 5).

Unfortunately, this more suitably probabilistic concept of fitness as average offspring contribution is still unsatisfactory. Our amended concept, like the original concept, is not explanatory. Offspring contribution and average offspring contribution are tallies, not causes, of the offspring contributions that lead to evolutionary success.

The offspring contribution of an organism of a particular type is much better explained in terms of particular traits of the organism in question: specific aspects of its physiology, anatomy, behavior, and so on, all of which contribute to its viability and fertility and ultimately to its overall *ability* to leave offspring in its particular environment. The most common construal of fitness in the philosophical literature today is one that identifies it with this ability and, ultimately, with the various properties that underlie this ability. This is the "propensity" interpretation of fitness (see, e.g., Brandon, 1978; Mills and Beatty, 1979; Burian, 1983; and Sober, 1984a).

The ability that is fitness bears a very special relationship to the abilities

that underlie it. The manner in which any type of organism achieves high fitness is ultimately a matter of the physiological, anatomical, and behavioral traits that underlie its viability and fertility and in turn underlie its overall descendant contribution ability. And yet different types of organisms achieve high fitness (and low fitness) in very different physiological, anatomical, and behavioral ways. For instance, what one accomplishes in terms of increased viability, another may accomplish in terms of increased fertility. And what one accomplishes in terms of increased viability by way of possessing a particular camouflaging pigment, another may accomplish by way of possessing a particular form of enzyme that increases metabolic efficiency. Moreover, the particular physiological and anatomical traits that lead to evolutionary success when "placed" in combination with other specific traits and in particular environmental circumstances may, in combination with a different set of traits and in different environmental circumstances, lead to evolutionary failure. So while each and every manifestation of high fitness (or low fitness) can be explained in terms of underlying physiological, anatomical, and behavioral traits, there seems to be no particular function of traits in terms of which fitness can universally be expressed. Rosenberg speaks of the "supervenience" of fitness upon its underlying causal components in his discussions of this aspect of fitness (1985, pp. 112–117, 164–169).

It is important to note that the propensity interpretation also has a probabilistic component that is intended to accommodate the fact that there may be a *range* of offspring contributions (rather than just one single number) within the reproductive capabilities of an organism of a particular type in a particular environment. It may be that within a particular environment, an organism of a particular type will, because of the combination of traits it has, most likely leave many offspring. And yet, in that same environment, there may also be a small chance of being struck by lightning, and hence a small chance of leaving no offspring at all.

This raises the problem of how to compare fitnesses. Proponents of the propensity interpretation forsake identifying the fitness of an organism or a type with an entire probability distribution of offspring contributions, and identify it instead with one number, namely, the arithmetic mean, or "expected value" (e.g., Brandon, 1978; Mills and Beatty, 1979). This is simply the weighted sum of the values of the various possible reproductive outcomes, where the appropriate weights are the probabilities of the various outcomes.

One apparent difficulty facing our original definition of "fitness" that the propensity interpretation does *not* resolve has to do with the supposed problem of the circularity of the principle of natural selection. To be sure, the claim that "the fittest are most likely to leave the most offspring" is a

tautology when "fittest" is defined in terms of actual offspring contribution. But the claim is no more empirical when "fittest" is defined as "best able to leave the most offspring."

The supposed tautology problem is really only a predicament, however, for those who believe that some such empirical principle is central to evolutionary theory. If some "principle of natural selection" were indeed the evolutionary equivalent of Newton's laws of motion, then one would expect to find it prominently placed in the standard textbooks; but it is not. Instead, one finds empirical formulae for predicting evolutionary outcomes based on assumptions about inheritance, with initial conditions covering fitness differences, population size, migration rate, mutation rate, and so on (basically, deductive consequences of the "Hardy-Weinberg law"). One formal axiomatization of evolutionary theory, by Mary Williams (1970), has a principle of natural selection as an axiom, though the principle is rendered empirical at the cost of treating "fitness" as an undefined primitive term.

There are a number of potentially more serious problems with the propensity interpretation of fitness. For instance, J. H. Gillespie (1972) has provided cogent reasons for suspecting that expected values of offspring contribution are not always appropriate for predicting and explaining evolutionary success. An analogy may help to make the point (Seger and Brockmann, 1987). A business may owe its long-term success to a costly insurance policy. The expense of the policy lowers the company's average yearly worth, but the policy itself considerably reduces the temporal variance in the company's worth and therefore helps prevent financial disaster. The business thus outlasts many competitors. In the case of evolution by natural selection, some types of organisms with relatively lower average numbers of offspring may prevail over types with relatively higher average numbers, as long as the former have smaller variances in offspring number and hence less chance of leaving no offspring at all—that is, less chance of evolutionary disaster. Gillespie argues that the evolutionary success of a type may represent a trade-off between the expected value and the variance of its probable offspring contributions (see also Gillespie, 1973, 1975, 1977). This means that the principle of natural selection, as stated above, with the expected-value version of the propensity interpretation of fitness inserted, is false, not circular. One way of construing the challenge now is to revise the definition of "fitness" along the line of Gillespie's suggestions, in order to maintain the circularity of the principle of natural selection!

Another problem with the propensity interpretation as usually elaborated is its emphasis on *offspring* contribution—its "shortsightedness," if you will. It is well known that, past a certain point, increased numbers of offspring can actually threaten the evolutionary success of a type, for example, by placing too great a demand on available resources or by min-

imizing the parental care that can be provided to each offspring. In these sorts of situations, more offspring may survive to leave more grand-offspring if there are fewer offspring in the first place. The literature on evolution of clutch size contains many such discussions (see, e.g., Lack, 1947b, 1954, 1966, 1968). To be sure, fitness as propensity to contribute offspring is positively correlated with very short-term evolutionary success—for example, with representation early in the life cycle of the next generation. But increased fitness, so construed, may be the very *cause* of decreased evolutionary success in the longer term.

The classic call for a long-term notion of fitness was by J. M. Thoday (1953). Some of his basic ideas have been recently recast in W. S. Cooper's (1984) interpretation of fitness as "expected time to extinction" (ETE). The ETE of a particular population or, more important, of a particular genotypic or phenotypic subpopulation, at a particular time and in a particularly specified environment, is just the probability-weighted sum of possible time intervals that might elapse before the (sub)population in question goes extinct. The most obvious problem with Thoday-Cooper notions of fitness is neatly recapped in the words of Keynes, who remarked that in the long run, "we are all dead." That is, what may concern us most is not *long-term* but, rather, more immediate evolutionary outcomes.

It might be possible to save the propensity interpretation by construing fitness as a "family" of propensities, including long-term and short-term descendant-contribution abilities, as summarized by a variety of different statistical parameters. It may be that different versions of the propensity interpretation will be appropriate under different circumstances. In this case, the concept will retain considerable intrinsic vagueness in spite of substantial technical elaboration.

FITNESS: REPRODUCTIVE AMBIGUITIES

Evelyn Fox Keller

A CHRONIC confusion persists in the literature of evolutionary biology between two definitions of individual fitness: one, the (average) net contribution of an individual of a particular genotype to the next generation, and the other, the geometric rate of increase of that particular genotype. The first refers to the contribution an individual makes to reproduction; the second refers to the rate of production of individuals. In other words, the first definition refers to the role of the individual as subject of reproduction, and the second to its role as object. The disparity between the two derives from the basic fact that, for sexually reproducing organisms, the rate at which individuals of a particular genotype are born is a fundamentally different quantity from the rate at which individuals of that genotype give birth—a distinction easily lost in a language that assigns the same term, "birth rate," to both processes.

Beginning in 1962, a number of authors have attempted to call attention to this confusion (Moran, 1962; Charlesworth, 1970; Pollak and Kempthorne, 1971; Denniston, 1978), agreeing that one definition—the contribution a particular genotype makes to the next generation's population—is both conventional and correct, and that the other (the rate at which individuals of a particular genotype are born) is not. Despite their efforts, however, the confusion persists (see Keller, 1987). In part this is because there remains a real question as to what "correct" means in this context or, more precisely, which definition is better suited to the needs the concept of fitness is intended to serve—in particular, the need to explain changes in the genotypic composition of populations. Given that need, we want to know not only which genotypes produce more but also the relative rate of increase of a particular genotype over the course of generations.

Perhaps not surprisingly, conflation of the two definitions of fitness is particularly likely to occur in attempts to establish a formal connection between the models of population genetics and those of mathematical

ecology. But because the standard models for population growth all assume asexual reproduction, the two formalisms actually refer to two completely different kinds of populations: one of gametic pools and the other of asexually reproducing organisms. I suggest that in attempting to reconcile these two theories, such a conflation may in fact be required to finesse the logical gap between them. A more adequate reconciliation of the two formalisms would seem to require both the introduction of the dynamics of sexual reproduction into mathematical ecology and the introduction of a compatible representation of those dynamics into population genetics.

Perhaps counterintuitively, it is probably the second—the inclusion (in population genetics models) of fertility as a property of the mating type—that calls for the more substantive conceptual shifts. Over the last twenty years, we have witnessed the emergence of a considerable literature devoted to the analysis of fertility selection—leading at least some authors to the conclusion that the “classical concept of individual fitness is insufficient to account for the action of natural selection” (Christiansen, 1983, p. 75).

When fertility selection *is* included in natural selection, the fitness of a genotype, like the fitness of a gene (as argued by Sober and Lewontin, 1982), is generally seen to depend on the context in which it finds itself. Here, however, the context is one determined by the genotype of the mating partner rather than by the complementary allele. A casual reading of the literature on fertility selection might suggest that the mating pair would be a more appropriate unit of selection than the individual, but the fact is that mating pairs do not reproduce themselves any more than do individual genotypes. As E. Pollak has pointed out, “even if a superior mating produces offspring with a potential for entering a superior mating, the realization of this potential is dependent upon the structure of the population” (1978, p. 389). In other words, in computing the contribution of either a genotype or a mating pair to the next generation’s population (of genotypes or mating pairs), it is necessary to take account of the contingency of mating in one’s consideration. Such a factor, measuring the probability that any particular organism will actually mate, will incur a frequency dependence reflecting the dependence of mating on the genotypic composition and structure of the entire population. Given the theoretical connections between frequency dependence and higher-level selection processes (see, e.g., Uyenoyama and Feldman, 1980), the inclusion of a full account of reproduction in evolutionary theory may well necessitate the conclusion that natural selection operates simultaneously on many levels (gene, organism, mating pair, and group)—not just under special circumstances, as others have argued, but as a rule.