

## CAN FITNESS BE AGGREGATED?

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The theory of evolution by natural selection depends on the concept of fitness, or selective value. Fitness has been defined in many ways: as the expected number of offspring in the long term, as the expected time to extinction, and as the absolute or relative numbers of offspring in the following generation or generations (Li 1955; Crow and Kimura 1970). Fitness has been formalized using selective coefficients (Haldane, Wright), the Malthusian parameter (Fisher), and in other ways (Prout 1965; Charlesworth and Charlesworth 1973; Slobodkin and Rapoport 1974). Darwin's concept of fitness and some of its offspring are reviewed by Mayr (1972, pp. 87–89).

A concept of fitness ought to make possible statements of the form, "under given circumstances,  $a$  is more fit than  $b$ ," when  $a$  and  $b$  are genotypes. In what follows, I will refer to the fitness of genotypes, but the general results in this paper do not depend on genetic mechanisms. They apply equally to the fitness of traits or of combinations of traits.

Studying the fitness of genotypes without reference to the ecology of the individuals with these genotypes is appropriate if the fitnesses of genotypes are homogeneous throughout the range of the species. Following Mayr's (1963, p. 415) classification of the ecological adaptations of species, a single ranking of fitness suffices for a species narrowly specialized for a single, constant environment or a number of identical, constant environments ("a very narrow niche"); or for a species of broadly tolerant individuals without genetic polymorphisms that permit specialized exploitation of extremes of the species' circumstances.

Species are found in, and display genetic adaptations to, environments that give the same genotype different selective values (Falconer 1960, pp. 43, 133, 322; types of species (3), (4), and (5) of Mayr 1963, p. 415; Karlin and McGregor 1972; see Felsenstein 1976 for a review of theoretical work). For example, of two strains of laboratory mice, one grows better than the other under good conditions, but worse under bad conditions (Falconer 1960, p. 133). Here the gain in weight is the measure of fitness. As another example, humans with a deficiency of glucose-6-phosphate dehydrogenase (G6PD) appear to have a survival advantage in malarial areas. G6PD-deficient individuals are susceptible to acute hemolytic anemia when

treated with oxidizing drugs such as antimalarial drugs, sulfa, and nitrofurantoin derivatives, and even aspirin. Consequently, G6PD-deficient individuals serving in the United States armed forces in malarial areas may suffer from prophylactic drugs as a result of the same G6PD-deficiency that is an advantage under different circumstances (Omenn and Motulsky 1978). There are so many other examples of this sort that Omenn and Motulsky use the term "eco-genetics" to describe "studies of genetically determined differences among individuals in their susceptibility to the actions of physical, chemical, and biological agents in the environment" (p. 83).

Call a ranking of genotypes by fitness in a particular population in a particular environment an *environmental fitness-ranking*. The central question of this paper is, Under what conditions is it possible to aggregate different environmental fitness-rankings into an overall ranking of genotypes by fitness, for the species? When environmental fitness-rankings can be aggregated, then the aggregated *species' fitness-ranking* can be studied as a function of genotypes only, without reference to particular environments and populations. When aggregation is not possible, then "fitness," by whatever criterion, cannot be understood without knowing the fitness of genotypes in the several environments in which the species occurs.

Another perspective on the same question is, If a species' fitness-ranking, aggregated from environmental fitness-rankings, must have certain specified properties, what kinds of species' fitness-rankings are possible? What species' fitness-rankings are consistent with desired properties of an aggregation procedure? This perspective replaces the question, "Can fitness be aggregated?" with the question, "When can fitness be aggregated?" In the extreme case, if the desired properties are inconsistent, then no aggregation is possible.

The logical relation between environmental fitness-rankings and a species' fitness-ranking aggregated from them does not seem to have been studied systematically. This omission may leave a student of evolution with the impression that there is no difficulty in finding an aggregation procedure that will have reasonable properties.

I propose below a set of six axioms to describe some desirable or plausible properties of the relations between a species' fitness-ranking and environmental fitness-rankings. Since this set of axioms is not self-consistent, no species' fitness-ranking satisfies these axioms. I consider some ways of restoring self-consistency to the axioms and some implications of the results for theories of fitness.

#### PROPOSED AXIOMS FOR FITNESS FUNCTIONS

Instead of referring to "particular populations in particular environments," I will speak of a species as divided into *econs*. By *econ*, I mean a local population or deme in its local environment. Two initially identical environments occupied by populations of different sizes and genetic compositions would be two different *econs*. Two initially identical demes (populations) in different local environments would also be different *econs*.

The six axioms may be stated informally and interpreted biologically. The axioms are numbered here to correspond with the formal statements of the axioms in the Appendix.

1. *The number of econs is finite and greater than one.*—This axiom assumes that there are at least two, but less than an infinite number of, populations of the species in different environments, or differing populations in similar environments.

2. *There are at least three genotypes.*—In a diploid species, this assumption is true if there is at least one heterozygous locus. If “genotypes” are traits, then there must be at least three traits.

3. *Whatever the environmental fitness-ranking of each econ, there is a species’ fitness-ranking which is uniquely determined by the environmental fitness-rankings.*—This axiom assumes that in a particular econ, it is possible to assign not necessarily a numerical value, but some ordering by fitness to the genotypes; and that whatever the environmental fitness-rankings, one for each econ, it is possible to aggregate the orderings in a unique way into a species’ fitness-ranking, which orders the genotypes by fitness without reference to econs.

4. *If genotype a is fitter than genotype b in every econ, then genotype a is fitter than genotype b according to the species’ fitness-ranking.*—This axiom assumes that the species’ fitness-ranking is consistent with the environmental fitness-rankings when they are unanimous about the relative fitness of two genotypes.

5. *In each econ, genotype a is fitter than genotype b, or vice versa; and there is a species’ ordering of a and b. Suppose the econs change in ways that affect the relative fitness of some other genotypes and possibly a and b, but in ways that leave the ordering between a and b exactly as they were before, in each econ. Then the relative ordering of a and b in the species’ fitness-ranking remains unchanged.*—For an example of the effect of axiom 5, suppose there are two econs and three genotypes, *a*, *b*, and *c*. Suppose that initially the first econ’s fitness-ranking orders the genotypes *c*, *a*, *b*; the second econ’s fitness-ranking orders the genotypes *a*, *c*, *b*; and the species’ fitness-ranking orders the genotypes *c*, *a*, *b*. If the first ordering changes to *a*, *b*, *c*, and the second changes to *c*, *a*, *b*, then the species’ fitness-orderings consistent with axiom 5 are *c*, *a*, *b* as before, or *a*, *c*, *b*, or *a*, *b*, *c*. In each of these orderings, the relative position of *a* and *b* is conserved because it was conserved in each econ, in spite of the shift in fitness of genotype *c*.

Axiom 5 asserts that only the rank order by fitness of two genotypes in the various econs determines the rank order by fitness of those two genotypes in the species’ fitness-ranking. If the rank orders are determined by numerical values resulting from some measurement or from some calculation based on measurements, axiom 5 asserts that any monotonically increasing function of the numerical values could serve just as well in the environmental fitness-rankings and should determine the same species’ fitness-ranking.

6. *There is no econ such that whenever one genotype is fitter than another in that econ, it is automatically fitter in the species’ fitness-ranking, regardless of the relative fitness of the two genotypes in all other econs.*—This axiom assumes more than one population or environment has some effect on the species’ fitness-

ranking. If, contrary to axiom 6, the relative fitness of genotypes in some single econ, a Garden of Eden, determined the relative fitness of genotypes for the species as a whole, the populations in the remaining environments would be irrelevant to overall fitness. Axiom 6 rules out this case because in this case there is no problem of aggregation to discuss.

To decide whether there exist environmental and species' fitness-rankings that satisfy these axioms, it is necessary to make the axioms formally precise. One way to do this, following Fishburn (1970), is presented in the Appendix. It can be proved that these axioms are inconsistent. This fact is known in economics as Arrow's impossibility theorem (Arrow 1963). The force of this theorem in population biology may be illustrated by examining some proposed species' fitness-rankings.

Before I present these examples, I want to make it clear that I am not accusing the following authors of having naive expectations of procedures for aggregating fitness, whether or not they may have proposed such procedures. Rather, by identifying the authors of models on which the following examples are based, I seek to avoid the opposite danger of not giving credit for models that are not originally mine.

#### FIRST EXAMPLE

Levins (1968, p. 18) considers a species that occurs in two environments,  $v = 1, 2$ . If the numerical fitness of a genotype  $a$  in econ  $v$  is given by  $W_v(a)$ , then  $a$  is fitter than  $b$  in environment  $v$  if and only if  $W_v(a) > W_v(b)$ . For a species' fitness-ranking in so-called "fine-grained" environments, Levins proposes a weighted average  $\bar{W} = pW_1 + qW_2$ , where  $p + q = 1$ ,  $0 < p < 1$ . This is interpreted to mean that  $a$  is fitter than  $b$  in the species as a whole if and only if  $\bar{W}(a) > \bar{W}(b)$ . With at least three genotypes, this species' fitness-ranking satisfies the first four axioms and the last. The way in which the fifth axiom is violated is instructive.

Levins does not specify the form of  $W_v$ . In proposing forms for  $W_v$ , I go beyond Levins' analysis to illustrate the main point of this paper.

One candidate for  $W_v$  is the net rate of reproduction  $R$ , where  $R(a)$  is the net rate of reproduction of genotype  $a$ . Another candidate is the intrinsic rate of natural increase  $r = (\ln R)/T$ , where  $T$  is the generation time. Let  $r(a)$  be the intrinsic rate of genotype  $a$ . Since  $r$  and  $R$  are monotonically increasing transformations of each other, they will yield the same ranking of any pair of genotypes if both genotypes have the same generation time  $T$ . Axiom 5 then requires that, for the above species' fitness-ranking,  $\bar{r} = pr_1 + qr_2$  and  $\bar{R} = pR_1 + qR_2$  should also provide the same ranking of any pair of genotypes. They do not.

For example, take  $p = 1/2$  and  $T = 25$  yr. Assume for the intrinsic rate  $r$  the values shown in table 1. These values are within the range of reason for human populations. According to table 1, the intrinsic rate  $r$  of genotype  $a$  in econ 1 is 0.001, and so on. Thus genotype  $b$  is fitter than genotype  $a$ , since  $\bar{r}(b) = 0.025 > \bar{r}(a) = 0.024$ . The net rates of reproduction implied by table 1 are shown in table 2. Genotype  $a$  is fitter than genotype  $b$  according to  $\bar{R}$ . This reversal in the ranking of  $a$  and  $b$  violates axiom 5. Similar reversals occur when some of the numerical

TABLE 1  
INTRINSIC GROWTH RATES  $r$  OF TWO GENOTYPES IN TWO ENVIRONMENTS

Genotype	Econ		Mean fitness $\bar{r} = (r_1 + r_2)/2$
	1	2	
<i>a</i>	.001	.047	.024
<i>b</i>	.030	.020	.025

TABLE 2  
NET RATES OF REPRODUCTION  $R$  OF TWO GENOTYPES IN TWO ENVIRONMENTS

Genotype	Econ		Mean fitness $\bar{R} = (R_1 + R_2)/2$
	1	2	
<i>a</i>	1.025	3.238	2.132
<i>b</i>	2.117	1.649	1.883

values assumed for  $r$  are negative; the possibility of reversal does not depend on all the values of  $r$  being positive.

This reversibility or instability of the weighted average is not necessarily a disabling weakness. Additional theory may indicate that only one form of the numerical function  $W_v$  is appropriate. Nevertheless, it would seem worthwhile to be aware of the possibility of reversals in a weighted-average species' fitness-ranking depending on the form of  $W_v$  chosen.

The intrinsic rate  $r$  and the net rate of reproduction  $R$  are monotonic functions of each other if the generation time  $T$  is constant from one genotype to another. If  $T$  varies, then reversals like the above in the rankings given by  $r$  and  $R$  can occur within a single econ.

Strobeck (1975) further discusses Levins' (1968) proposals for "fine-grained" environments.

#### SECOND EXAMPLE

Levene (1953) proposed, and Li (1955) analyzed further, a model of a species that occurs in  $k$  localities (here, econs). At a single locus, alleles  $A_1$  and  $A_2$  have relative frequencies  $p$  and  $q$ , respectively, at the zygotic stage of the life cycle ( $p + q = 1$ ). These frequencies are the same in the species and in each econ. In the  $i$ th locality, the genotypes  $A_1A_1$ ,  $A_1A_2$ , and  $A_2A_2$  have (nonnegative) relative selective values  $W_{11}^{(i)}$ ,  $W_{12}^{(i)}$ , and  $W_{22}^{(i)}$ , which are applied to the corresponding genotypic frequencies (the same in each locality)  $p^2$ ,  $2pq$ , and  $q^2$ . After selection, the survivors from all localities form a pool that mates randomly. The proportion of this pool that consists of the survivors from the  $i$ th locality is  $c_i \geq 0$  (with  $\sum_i c_i = 1$ ).

Li (1955, p. 287) defined “the average fitness of the entire population” as

$$\bar{W} = \prod_{i=1}^k [p^2 W_{11}^{(i)} + 2pq W_{12}^{(i)} + q^2 W_{22}^{(i)}]^{c_i}. \quad (1)$$

This quantity will be interpreted below as a possible species’ fitness-ranking. Li proved that equilibrial values  $q^*$  of the gene frequency  $q$  correspond to (local) maxima or minima of  $\bar{W}$ . If  $\bar{W}(q^*)$  is a local maximum,  $q^*$  is locally stable; if  $\bar{W}(q^*)$  is a local minimum,  $q^*$  is locally unstable. This result has been greatly generalized and extended (Felsenstein 1976, pp. 258–275).

In the case of a single locality,  $k = 1$ , the selective values are constant for the entire species. Equation (1) reduces to the classical mean-fitness function, which is a parabolic function of  $q$ . When  $k = 1$  (see Li 1955, p. 282, for references), there is an equilibrial point  $q^*$  satisfying  $0 < q^* < 1$  if and only if  $W_{11} - W_{12}$  and  $W_{22} - W_{12}$  are either both negative or both positive; in the former case,  $q^*$  is a stable equilibrium, and in the latter,  $q^*$  is an unstable equilibrium. Here I have dropped the superscripts on  $W_{ij}$  since there is only one locality. For species that occur in a single locality, the mean-fitness function is thus a valid criterion for inferring when the heterozygote is the fittest genotype. It is convenient to state this criterion formally.

*Criterion: If  $\bar{W}(q)$  has a unique global maximum at  $q = q^*$  such that  $0 < q^* < 1$ , then the heterozygote genotype  $A_1A_2$  is fitter than either homozygote, and conversely.*—Could this criterion be used to rank the fitness of the heterozygote relative to the other genotypes for species that occur in more than one locality? The conjecture that the criterion could define a species’ fitness-ranking must not be attributed to either Levene (1953) or Li (1955). It follows from a suggestion, made to me in correspondence by an evolutionary population biologist of distinction, that equation (1) may serve as a species’ fitness-ranking for a species that occurs in several localities.

Figure 1 shows  $\bar{W}$  of a species that occurs in two localities ( $k = 2$ ).  $\bar{W}$  has a unique global maximum at  $q^*$  satisfying  $0 < q^* < 1$ . Applying the above criterion leads to the conclusion that the heterozygote is fitter than either homozygote in the species as a whole. According to the parameters for figure 1, however, in both localities, the heterozygote has lower relative fitness than the  $A_2A_2$  homozygote, even though the “average fitness of the entire population” is maximal at  $q^*$  such that  $0 < q^* < 1$ ! Thus, if the criterion based on  $\bar{W}$  were taken as part of the specification of a species’ fitness-ranking, axiom 4 (unanimity) would be violated. The only difference from the example of Levene and Li is that, in figure 1,  $c_1 = 0.6$ ,  $c_2 = 0.4$  (instead of their  $c_1 = c_2 = 0.5$ ).

In a graphically more dramatic example, which is qualitatively no different (fig. 2), again the “average fitness of the entire population” is maximal at  $q^*$  such that  $0 < q^* < 1$ , while the  $A_2A_2$  homozygote is fitter than the heterozygote in each of two localities. (Again  $\bar{W}$  has a local minimum at  $q$  such that  $0 < q < 1$ , though the minimum is much less pronounced than in fig. 1.)

This second example shows that the difficulty in constructing a species’ fitness-ranking that satisfies all six axioms does not disappear when migration is permitted among the econs in a dynamic model.

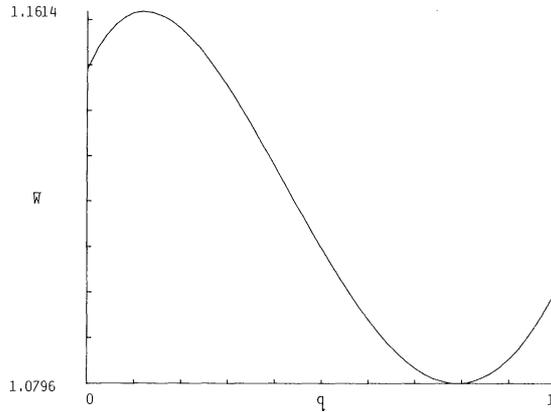


FIG. 1.—Mean fitness  $\bar{W}$  given by eq. (1) as a function of  $q$ . There is a unique global maximum at a value  $q^*$  satisfying  $0 < q^* < 1$ , although the heterozygote has lower fitness than one of the homozygotes in both localities. Parameter values:  $k = 2$ ,  $W_{11}^{(1)} = 2$ ,  $W_{12}^{(1)} = 1$ ,  $W_{22}^{(1)} = 1.1$ ,  $W_{11}^{(2)} = 0.5$ ,  $W_{12}^{(2)} = 1$ ,  $W_{22}^{(2)} = 1.1$ ,  $c_1 = 0.6$ ,  $c_2 = 0.4$ .

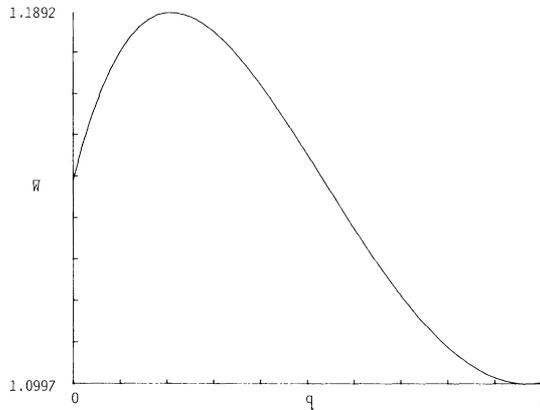


FIG. 2.—Mean fitness  $\bar{W}$  given by eq. (1) as a function of  $q$ . As in fig. 1, there is a unique global maximum at a value  $q^*$  satisfying  $0 < q^* < 1$ , although the heterozygote has lower fitness than one of the homozygotes in both localities. Parameter values:  $k = 2$ ,  $W_{11}^{(1)} = 2$ ,  $W_{12}^{(1)} = 1.09$ ,  $W_{22}^{(1)} = 1.1$ ,  $W_{11}^{(2)} = 0.5$ ,  $W_{12}^{(2)} = 1.09$ ,  $W_{22}^{(2)} = 1.1$ ,  $c_1 = 0.6$ ,  $c_2 = 0.4$ .

The function (1) does just what Li (1955) constructed it to do: it predicts the stable stationary points of  $q$  as the locations of its local maxima. As a species' fitness-ranking, however, (1) has properties that might reasonably be regarded as implausible.

#### THIRD EXAMPLE

A reasonable counterattack to the preceding example is to say that the sole purpose of defining a species' fitness-ranking is to construct a potential function

that will describe where the genetic composition of the population will settle; the axioms are irrelevant. The next example shows concretely that species' fitness-rankings are sometimes constructed for purposes other than predicting the equilibrium genetic composition of an evolving population. It therefore becomes sensible to specify, as the above axioms attempt to do, some desirable general properties for species' fitness-rankings. I owe this example and the references on which it is based to Timothy Prout.

Agronomists have observed that the yield (seeds harvested per seed planted) of one variety of wheat, say Baart, is different when a Baart plant is surrounded by other Baart plants from when a Baart plant is surrounded by plants of the wheat variety Poso (Allard and Adams 1969). For a set of  $k$  varieties, they have systematically measured the yield, or "fitness,"  $w_{ij}$  of variety  $i$  when surrounded by variety  $j$ . From experiments in which plants of variety  $i$  are surrounded by a mixture of varieties, they have inferred that the effect of the mixture on the yield of variety  $i$  is the weighted sum of the solo effects on the yield of variety  $i$  of each of the surrounding varieties, with weights equal to the proportion of each of the varieties in the surrounding mixture. If  $p'$  is the row vector  $(p_1, p_2, \dots, p_k)$  of proportions of the varieties in a homogeneously mixed field, the yield per plant of variety  $i$  is

$$w_i = \sum_{j=1}^k p_j w_{ij}. \quad (2)$$

Since the varieties are essentially selfing or autogamous, the composition of the population evolves like that of a haploid population until, at equilibrium, the mean yields per plant of each variety are all equal to each other and to the overall mean yield per plant, namely,  $p'Wp$  (see, e.g., Cockerham and Burrows 1971, p. 15, for the analysis). The equilibrium proportions  $p^*$  satisfy, for some scalar constant  $K$ ,

$$Wp^* = K\mathbf{1} \quad (3)$$

where  $\mathbf{1}$  is the column vector with each element equal to 1.

In my terms, each variety corresponds to one "genotype," though some of the varieties may in fact be genetically heterogeneous. Each column of the yield matrix  $W = (w_{ij})$  defines one environmental fitness-ranking, namely, the fitness of each variety  $i$  when surrounded by an otherwise pure "environment" of variety  $j$ . Equation (2) gives a species' fitness-ranking, which ranks the aggregated yields of each variety. The equilibrium proportions  $p^*$  are adjusted so that the yield per plant is the same for every variety.

Unlike the evolutionist and agricultural geneticists, who are interested in the evolution and equilibria of a mixed stand, the agronomist seeks to maximize the yield of grain, which is proportional to  $p'Wp$ . The vector of proportions that maximize yield, denoted by  $\bar{p}$ , satisfies (Cockerham and Burrows 1971, p. 22), for some scalar constant  $c$ ,

$$(\frac{1}{2})(W + W')\bar{p} = c\mathbf{1} \quad (4)$$

where  $W'$  is the transpose of the matrix  $W$ , and  $\mathbf{1}$  is the vector of 1's as before.

Under the condition (4) of maximal yield, the mean yield per plant of variety  $i$  is given not by (2) with  $p = \bar{p}$  but by

$$\bar{w}_i = \sum_{j=1}^k p_j (w_{ij} + w_{ji}) / 2 \quad (5)$$

with  $p = \bar{p}$ . One may view  $\bar{w}_i$  as a species' fitness-ranking invoked for the purpose of maximizing yield rather than predicting equilibrium.

The two species' fitness-rankings (2) and (5) will give identical rankings of the aggregate fitness of the varieties if the fitness matrix  $W$  is symmetric, because in this case (5) is just (2).

If  $W$  is not symmetric, it is easy to construct examples with just  $k = 2$  varieties in which the rank orders of the varieties differ. For example, if

$$W = \begin{bmatrix} 1 & 5 \\ 3 & 2 \end{bmatrix},$$

at equilibrium the proportions of the two varieties will be  $p^* = (0.6, 0.4)$  while maximal yield will be obtained by the proportions  $\bar{p} = (0.4, 0.6)$ . When  $p = p^*$ ,  $w_1 = w_2$  (as required) but  $\bar{w}_1 < \bar{w}_2$ . When  $p = \bar{p}$ ,  $w_1 > w_2$ , but  $\bar{w}_1 = \bar{w}_2$  (as required). When  $p = (0.5, 0.5)$ , which is neither equilibrial nor of maximal yield,  $w_1 > w_2$  and  $\bar{w}_1 < \bar{w}_2$ .

This example should dispel the notions that every biological problem has a unique "natural" species' fitness-ranking, and that the "natural" species' fitness-ranking is the potential function that the dynamics of the problem maximize or minimize. On the contrary, different species' fitness-rankings are constructed for different purposes.

#### WHICH AXIOM TO ABANDON?

The point of the examples and the preceding theory is that any proposed species' fitness-ranking must violate at least one of the six axioms. One possible response to this conclusion is to reject one or more of the axioms. For example, if one had a strong theoretical argument for a particular numerical measure of fitness, one might object to axiom 5 because it neglects quantitative differences in fitness between genotypes.

Instead of using a weighted mean with fixed weights, considered in the first example, one might weight the fitnesses in two econs by the population sizes in the two environments. This weighting would depend dynamically on the fitnesses in each econ, because the fitnesses determine the rates of change of the numbers of individuals of each genotype in each econ. This alternative species' fitness-ranking, however, violates axiom 3, because the weak order of genotypes for the species is no longer completely determined by the weak orders of genotypes in the separate econs.

Fishburn (1970) proves that the six axioms are inconsistent by showing that

the last five axioms imply that the first axiom is false. Hence, another escape from the inconsistency of the axioms is to assume, contrary to axiom 1, that there is an infinite number of econs.

Under the definition of econ, two physically identical environments occupied by populations with differing relative frequencies of the genotypes  $a$  and  $b$  might be treated as different econs. Since there is an infinity of different relative frequencies of the genotypes, an infinity of potential econs makes sense. When the frequency of a genotype in a population changes, the population in its environment becomes another econ, to which another fitness-ranking applies.

Unfortunately for this avenue of escape from Arrow's impossibility theorem, there is still a problem when there are infinite econs. If the set of econs has the structure of an atomless measure space (see Kirman and Sondermann 1972 for a definition), there always exists a subset of the econs that can act collectively as a Garden of Eden, and this subset may be chosen as an arbitrarily small proportion of all econs (Kirman and Sondermann 1972). In effect, the species' fitness-ranking can be determined by unanimity of the environmental fitness-rankings in an arbitrarily small proportion of econs.

Arrow's proof that the six axioms are inconsistent shows that the first five axioms imply that axiom 6 is false. To remove the inconsistency of the axioms, one may assume, contrary to axiom 6, that the environmental fitness-ranking of some Garden of Eden fixes the species' fitness-ranking. Then the fitness-ranking of the Garden of Eden may be studied as a function of genotypes only, without reference to other econs.

Another way to escape the constraints of the impossibility theorem is to examine the fine print of the definition of fitness-rankings (Appendix). It may be shown (Blair and Pollak 1979, 1983) that the definition of weak order used for fitness-rankings is equivalent to supposing that both strictly greater fitness and indistinguishable fitness are transitive relations. It seems reasonable to suppose, as the transitivity of strictly greater fitness assumes, that if  $a$  is strictly fitter than  $b$ , and  $b$  is strictly fitter than  $c$ , then  $a$  is strictly fitter than  $c$ . It seems less certain, as the transitivity of indistinguishable fitness assumes, that if  $a$  and  $b$  do not have distinguishable fitness, and  $b$  and  $c$  do not have distinguishable fitness, then necessarily  $a$  and  $c$  do not have distinguishable fitness.

Abandoning the transitivity of indistinguishable fitness allows an escape from Arrow's impossibility theorem, at a price: if any two econs rank the relative fitness of  $a$  and  $b$  oppositely, then the species' fitness-ranking must rank  $a$  and  $b$  as having indistinguishable fitness (Blair and Pollak 1983, p. 91, where the result is attributed to A. K. Sen). Since a species' fitness-ranking is supposed to assess the relative fitness of two genotypes when different econs rank them oppositely, a species' fitness-ranking that always says such pairs of genotypes are indistinguishable in fitness is not a very useful escape from Arrow's impossibility theorem.

Other classes of species' fitness-rankings become possible when Arrow's axioms are weakened in various ways. For example, it seems biologically plausible to consider abandoning neutrality. Neutrality requires that if  $a$  and  $b$  have the same relative rank as  $x$  and  $y$  in every econ, then  $a$  and  $b$  have the same relative

rank in the species' fitness-ranking as  $x$  and  $y$ , for all genotypes  $a$ ,  $b$ ,  $x$ , and  $y$ . It seems reasonable that if  $a$  and  $b$  differ only in alleles that govern some character of minor selective importance, perhaps eye color, while  $x$  and  $y$  differ in alleles of major selective significance, then the rule for ordering  $a$  and  $b$  in the species' fitness-ranking could differ from the rule for ordering  $x$  and  $y$ . Such a difference in rules would violate neutrality.

As a second example, the assumption that the aggregation procedure must be prepared to deal with any arbitrary ordering of genotypes in econs might be abandoned in favor of the less general assumption that some or all econs admit only one or a few possible orderings of genotypes. Genotypes with alleles that are not lethal prior to reproduction might always be fitter than genotypes with prereproductively lethal alleles, for example.

Even if one abandons Arrow's assumption (in biological translation) that a species' fitness-ranking must work for every logically possible combination of environmental fitness functions, and assumes instead that a species' fitness function is only required to work for a given particular combination of environmental fitness-rankings, severe problems of inconsistency remain if the environmental fitness-rankings are sufficiently diverse (Pollak 1979).

Blair and Pollak (1982, 1983) extend and review studies of the species' fitness functions ("collective choice rules," in their language) that become possible when Arrow's axioms are relaxed. Their conclusion, that "there is little comfort here for those designing ideal procedures" (1983, p. 95), applies with force to attempts to construct species' fitness-rankings.

#### CONCLUSION

The problem of constructing a species' fitness-ranking from environmental fitness-rankings is a problem of aggregation. Aggregation has been recognized as a pervasive problem in the social sciences. Its formal structure has been studied extensively (Ijiri 1971). Aggregation is equally pervasive in population biology and it is beginning to be recognized and studied (O'Neill and Rust 1979; Cale and Odell 1979, 1980; Gibberd 1981; Gardner et al. 1982; Cale et al. 1983). Here I have suggested six axioms that describe potentially desirable features of a species' fitness-ranking. As a consequence of Arrow's impossibility theorem, no species' fitness-ranking can have all of these desirable properties.

What is the practical benefit of knowing this? The impossibility of satisfying all six axioms serves as a reminder to make sure that the axioms sacrificed by a chosen species' fitness-ranking are not essential to the purpose of the species' fitness-ranking. (E.g.,  $\bar{W}$  in [1] locates the equilibria of the gene frequency  $q$ ;  $\bar{W}$  does not assess the relative fitness of genotypes within individual localities.) This reminder may be especially valuable for human populations, in which the fitness of genotypes often depends strikingly on the environment (Omenn and Motulsky 1978).

A measure of fitness makes sense only as part of some more extensive theory about the population dynamics of genetically diverse organisms. The appropri-

ateness of a measure of fitness is determined by the purpose and by the success or failure of the larger theory in which it is embedded.

## SUMMARY

A fitness-ranking compares the fitness of two genotypes or, more generally, traits. A *species' fitness-ranking* describes the relative fitness of genotypes in an aggregated species as a whole. An *environmental fitness-ranking* describes the relative fitness of genotypes in a particular population of the species in a particular environment. A set of axioms is proposed to describe what might plausibly be desired of the relation between a species' fitness-ranking and environmental fitness-rankings. There is no way in general to construct a species' fitness-ranking that satisfies all of these axioms. Hope that a single natural measure of the "fitness" of genotypes exists for a species as a whole must be replaced by attention to the dynamics of multiple populations in multiple environments.

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## APPENDIX

## FORMAL STATEMENT OF AXIOMS

I use exactly the notation of Fishburn (1970), who gives a proof and economic interpretation of Arrow's theorem. Let  $X$  be the set of genotypes  $a, b, c, \dots$  and let  $V$  be the set of econs such as  $v$ . A weak-order  $P$  on  $X$  is defined as a binary relation on  $X$  which is asymmetric (if  $aPb$ , then not  $bPa$ ) and negatively transitive (if not  $aPb$  and not  $bPc$ , then not  $aPc$ ). Each fitness-ranking is assumed to be a weak order, where  $aPb$  has the interpretation "genotype  $a$  is fitter than genotype  $b$ ."

Let  $W$  be the set of all weak orders (fitness-rankings) on the set  $X$  of all genotypes. Let  $F$  be the set of all functions, such as  $f$  and  $g$ , on  $V$  (the set of econs) into  $W$ . That is, for  $f$  in  $F$  and  $v$  in  $V$ ,  $f(v)$  is the environmental fitness-ranking for econ  $v$  assigned by  $f$ .  $f(v) = g(v)$  on  $\{a, b\}$  means that  $af(v)b$  if and only if  $ag(v)b$  and that  $bf(v)a$  if and only if  $bg(v)a$ .  $f = g$  on  $\{a, b\}$  means that, for all  $v$  in  $V$ ,  $f(v) = g(v)$  on  $\{a, b\}$ .  $|A|$  is the cardinality (number of members) of the set  $A$ .

The formal statement of the 6 axioms follows.

1. Econs, or population-environment pairs:  $|V|$  is some positive integer  $> 1$ .
2. Genotypes:  $|X| \geq 3$ .
3. Species' fitness-ranking:  $\sigma$  is a function on  $F$  into  $W$ .

4. Unanimity: For all  $a, b$  in  $X$  and all  $f$  in  $F$ , if  $af(v)b$  for all  $v$  in  $V$ , then  $a\sigma(f)b$ .
5. Independence: For all  $a, b$  in  $X$  and all  $f, g$  in  $F$ , if  $f = g$  on  $\{a, b\}$ , then  $\sigma(f) = \sigma(g)$  on  $\{a, b\}$ .
6. No Garden of Eden: There is no  $v$  in  $V$  such that, for all  $a, b$  in  $X$  and all  $f$  in  $F$ , if  $af(v)b$  then  $a\sigma(f)b$ .

A reformulation (Fishburn 1970) of Arrow's impossibility theorem (1963) asserts that these 6 axioms are inconsistent.

Arrow (1963) and Blau (1957) formulate the definitions and theorem differently. A binary relation  $P$  on  $X$  that satisfies Fishburn's definition of weak order is also transitive and satisfies ([not  $bPa$  and  $bPc$ ] or [ $aPb$  and not  $cPb$ ]) implies  $aPc$  (Fishburn 1970, p. 104), and hence has the properties required of the weak orders of Blau and Arrow.

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