

A COMPETITIVE SELECTION MODEL

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Manuscript received January 19, 1973

Revised copy received April 16, 1973

Transmitted by TIMOTHY PROUT

ABSTRACT

The proportionate contribution of a genotype to the next generation is not independent of frequency and cannot always safely be equated with a constant. *Survival potential* (HALDANE's *viability*) permits the use of a genetic selection model which deals more realistically with competition. A broader property than survival potential, called *fitness potential*, should be distinguished from fitness, which it determines in a competitive context.

THE general selection model attempts to describe changes in allele frequencies and in genotype frequencies, resulting from selection; it incorporates as a fundamental feature a constant, frequency-independent selection coefficient for each genotype. This means that, irrespective of the relative size of a genotypic class, the proportion of its members surviving to reproduce will be constant relative to the surviving proportions of the other genotypic classes. I believe this feature to be in error, and in conflict with reasonable concepts of competition. I should like to recall a model of HALDANE's (1931).

In HALDANE's model the members of any genotypic class are distributed normally with respect to what he called *viability*, and those individuals with the higher viabilities survive.* The selection threshold (the minimum viability permitting survival) is determined by the total distribution for the entire population and by the proportion of zygotes in the population that survive to reproduce. I envision conditions that are constant except for the frequency of the genotype in question; thus, the distribution of phenotypic values within a genotype remains constant.

Consider a population composed of two genotypic classes of beans, *aa* and *A-* (*AA* or *Aa*). The first has a mean weight of 9 g, the second, 10 g. Standard deviation in each case is 1 g. Suppose we want to save the heaviest 5% of seed.

In Figure 1, two cases are illustrated. In the first, 80% of the individuals are *aa*, and 20% are *A-*. The threshold for selection of the heaviest 5% in the entire population turns out to be at 10.995 g, as will be explained shortly. The hatched areas represent the selected beans. Whether a bean will be selected or not depends on the rank of its weight.

* In later papers, HALDANE adopted a different use of *viability*, essentially synonymous with *survival rate*, as used here. This conforms to the definition given in King's *Dictionary of Genetics* (Oxford University Press, 1972); his earlier usage is similar to the definition given in RIEGER, MICHAELIS, and GREEN's *Glossary of Genetics and Cytogenetics* (Springer-Verlag, 1968).

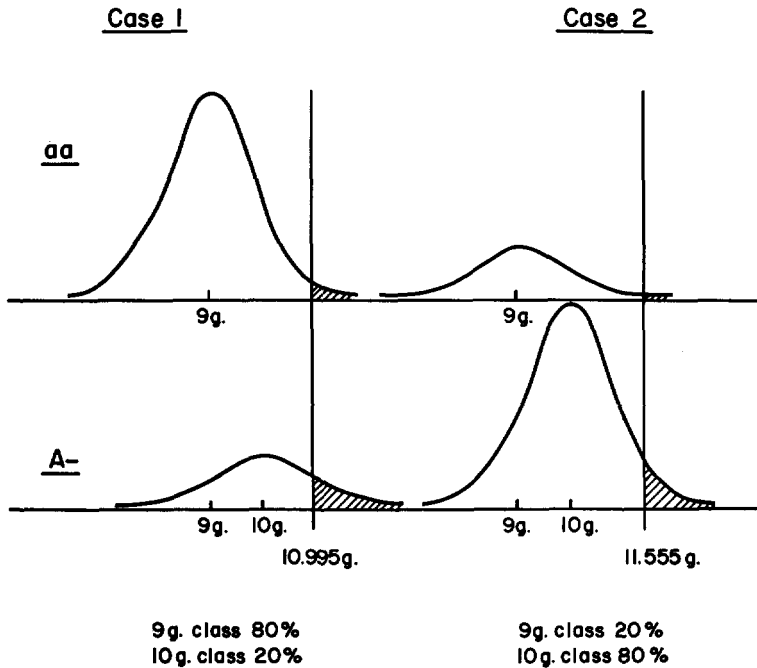


FIGURE 1.—Two cases of truncation selection involving a population composed of two genotypic classes, *aa* (mean weight 9g) and *A-* (mean weight 10g). The cases differ in the proportions of the classes. In each case, the heaviest 5% are selected.

In the second case, 20% of the individuals are *aa* and 80% are *A-*. Since there are more beans of the heavier class, the competitive standard is higher. The minimum weight selected is greater. The threshold is now at 11.555 g. The result of these changes is a striking difference in the relative survival rate of the light (*aa*) and heavy (*A-*) classes.

This may not be visually obvious, since we must compare ratios of ratios. To begin with, we consider the first case. What proportion of the *aa* individuals survive? It can be estimated using a normal distribution table (e.g., BEYER 1966) that 0.023 survive. This estimation is made by determining the position of the common threshold that will cut off 0.05 of the combined classes. We also find that 0.160 of the less numerous but heavier *A-* class survive. According to standard practice, we set the survival rate of the "better" class at 1, and so the relative survival rate of *aa* is $0.023/0.160 = 0.144$. Adaptive values are routinely calculated this way. (The assumption in the past has been that they are frequency-independent.)

We now have obtained the relative survival rate of *aa*, a ratio of ratios or a ratio of proportions, namely, 0.023 (proportion of *aa* surviving): 0.160 (proportion of *A-* surviving). We turn now to the second case, where the heavier genotypic class (*A-*) has now become the more numerous class as well. Using the position of the new 5% threshold, we can find that only 0.0055 of the *aa*

individuals will now survive. A smaller proportion of $A-$ individuals also survives, 0.0610. [It is instructive to check this result: $0.020 \times 0.0055 + (0.80 \times 0.0610) = 0.0499 = 0.05$.]

Now taking the ratio of these proportions, we find that the relative survivorship of aa is $0.0055/0.0610 = 0.090$. Finally, we compare this result with the relative survival rate pertinent to the previous case, 0.144. The relative survival rate has dropped from 0.144 to 0.090 as the frequency of the heavier class has increased from 0.20 to 0.80. These values are determined, of course, by the additional information that the weights of the two classes are normally distributed, with equal standard deviations, and with means one standard deviation apart. Note that a given selection threshold determines a unique ratio of two survival proportions.

So, only when the selection threshold remains constant can a constant proportion of a genotypic class survive. But the selection threshold is unlikely to remain constant during natural directional selection, as the "best" class becomes more numerous. A constant threshold would mean increased survival rate; this could not go on indefinitely. Rather, the standard will become more stringent, at the increased expense of the "poorest" class.

This example calls to mind an observation made by HALDANE (1932), who pointed out that relative survival rate (his "intensity of selection") depends on the amount of culling (his "intensity of competition"), and also on variances of the competing classes. Indeed, above a certain intensity of selection, the class with the lower mean but higher variance is favored. But neither HALDANE nor FALCONER (1960) nor CROW and KIMURA (1970) have explicitly considered variation of the selection coefficient as a function of the frequencies of competing classes or genotypes. LERNER (1958) discusses the subject in ways unrelated to the present topic.

We may now ask whether it is proper to attribute frequency independence to selection coefficients of the *magnitudes commonly discussed*. Let us consider a population of constant size and constant overall survival rate per generation. In place of weight, the only significant phenotypic attribute of the beans in our previous example, we shall substitute a property which plays the same role. Its rank, together with a threshold rank, determines whether an individual will survive or not. We shall call this property *survival potential*. To know whether an individual will survive, we must know the rank of its survival potential (in the competitive situation in which we see it) and the threshold rank. With two genetic classes having equal variances but different means, it is possible to calculate relative survival rates under two extreme conditions: overwhelming abundance of the poorer class, and overwhelming abundance of the better class. We must specify the overall survival rate (which we have said holds in both conditions) and the relative survival rate found in one of the two cases. The results of some calculations are listed in Table 1.

To work through an example, we shall specify an overall survival rate of 0.2. We shall also specify that when the inferior class is overwhelmingly abundant, its relative survival rate is 0.5. What is it when the superior class is overwhelm-

TABLE 1

Relative survival rate of the poorer class vs. overall survival rate and stage of selection

Initial relative survival rate	Final relative survival rate				
	0.5	0.2	Overall survival rate 0.1	0.05	0.01
0.90	0.89	0.89	0.90	0.90	0.90
0.80	0.76	0.78	0.79	0.79	0.79
0.70	0.57	0.66	0.67	0.68	0.69
0.63*	0.41	0.57	0.59	0.60	0.61
0.60	0.33	0.52	0.55	0.57	0.58
0.50	...	0.38	0.43	0.45	0.47
0.40	...	0.23	0.29	0.33	0.36
0.30	...	0.09	0.17	0.20	0.24
0.20	...	...	0.05	0.09	0.13
0.10	...	...	...	0.01	0.04

* cf. METTLER and GREGG (1969), p. 105.

ingly abundant? To find out, we first determine the difference between the mean survival potential of the superior class and that of the inferior class.

When the inferior class constitutes practically the entire population, 0.2 of the inferior class survives. Of the few superior genotypes $0.2/0.5 = 0.4$ survive. We now see, by consulting a normal distribution table, that the selection threshold for the inferior genotype is 0.842 standard deviation units from the mean; for where $1 - F(x) = 0.200$, $x = 0.842$. This same threshold is 0.253 standard deviation units from the mean for the superior group; again, where $1 - F(x) = 0.4$, $x = 0.253$. Thus the means are $0.842 - 0.253 = 0.589$ units apart.

When the superior class is overwhelmingly abundant, 0.2 of this class survives, and the threshold is of course 0.842 units from its mean. For the inferior genotype, the threshold must be $0.842 + 0.589 = 1.431$ units from its mean, corresponding to an absolute survival rate of 0.0765. Where $x = 1.431$, $1 - F(x) = 0.0765$. In this case, therefore, the relative survival rate of the inferior genotype is $0.0765/0.20 = 0.38$, as opposed to the previous value, set at 0.50.

Obviously, the two cases just described correspond to times very early and very late in a process of selection. Thus, a relative survival rate of 0.50 characteristic of an abundant inferior genetic class decreases to 0.38 as the inferior class becomes scarce. And this is a general feature: *As selection proceeds, the relative performance of the inferior genotype always becomes poorer*, though not always substantially poorer. Table 1 lists some "initial" and "final" relative survival rates determined in this way. Clearly, there is a range of commonly employed values where the use of the constant adaptive value is a perfectly good approximation.

In this model, the variance of the two populations is identical; were it made proportional to the mean, the principle would not change: for any set of normal distributions with different means, each common threshold is associated with a unique ratio of above-threshold fractions.

It is also conceivable that the variance in survival potential within a genotypic class decreases (during the replacement of one such class by another) due to the

fixation of alleles at other loci that make for high survival potential. If this happens, then the genotypes in question become relatively more important; and the difference in mean competitive values, as measured in standard deviation units, increases. This would of course enhance the progressive decline in the relative survival rate of the poorer class.

We have considered the selection coefficient only as a function of survival, a convenient but incomplete treatment. Since reproduction is generally a major variable, we may term *reproductive potential* the reproductive property analogous to survival potential. Reproductive potential will be a factor determining the quantity of offspring produced. In this view, the quantity of offspring produced bears no constant relationship to reproductive potential but depends as well on the competitors' reproductive potential.

The introduction of quantitative variation in reproduction means that no treatment that considers reproduction can be as simple as a consideration of survival alone. This is of course not a new problem, and most elementary discussions of selection models consider survival only.

In any event, the overall reproductive rate cannot change without causing a change in population size, all other things remaining equal. But if a particular genotype, characterized by an above-average reproductive rate, rises in frequency, the overall reproductive rate will rise. Thus, if population size is to remain constant, reproductive rate cannot be constant for a given genotype while that genotype is rising in frequency in response to selection for increased reproductive rate. The reproductive rate of the selected genotype will have to decrease.

As fitness is a combination of survival and reproductive rates, we might define *fitness potential* as the combination of survival potential and reproductive potential; it is the quantitative property upon which fitness depends in the light of the competition. This is a small step: we leave unanswered how survival potential and reproductive potential should be combined (no biologist would expect them to be independent), and we have not specified the mathematical relationship between fitness potential and fitness.

Non-genetic factors of course, in most cases will help determine fitness potential (via both survival potential and reproductive potential). Using survival

TABLE 2
Relationship of terms used

Genetically determined variate*	Individual	Competitively determined result Class
Survival potential	Survival or death†	Survival rate
Reproductive potential	Number of offspring	Reproductive rate (Average number of offspring)
Fitness potential	Fitness‡	Fitness‡

* Constant environment assumed.

† All results except individual survival/death can be stated both in absolute and in relative terms.

‡ Proportionate contribution to the next generation.

potential as an example again, we can consider a strict division between life and death at some threshold value. With regard to the genotype itself, the division will clearly be blurred: near-threshold genotypes especially will have probabilities of survival between 0 and 1. Among other things, the distinction between selection of phenotypes and selection of genotypes should be reaffirmed.

It will be noted that the frequency-dependent selection described here is not the kind that would favor the maintenance of polymorphism in a population, because rarity of either type decreases rather than increases its selective advantage relative to the other type.

Finally, truncation selection of the form described is not universal. Unconditional lethals constitute one exception. Also, the following truisms may be noted: to the extent that the differential effects on fitness of the alleles at a given locus are independent of competition, those alleles are not subject to competitive truncation selection. And to the extent that the effects on fitness of the allele sets at two loci are independent of one another, they are not subject in common to the same process of truncation selection.

CONCLUSIONS

First, one must be cautious in assuming constant selection coefficients. Second, it is probably a step in the right direction to use a variate such as fitness potential for a point of departure, as HALDANE did with viability. Granting the variability of environmental and other factors, fitness potential is nevertheless one step closer to constancy than selection coefficient. Finally, it must be remembered that fitness is a result, and fitness potential is causally antecedent to fitness. The two ought not be confused.

This work has been supported in part by a grant from the National Science Foundation to the program for the biological sciences at The University of Iowa and by PHS Grant GM 18967-01 from NIH. I am grateful to MARTHA BAYLOR, CLARK COCKERHAM, JOSEPH P. HEGMANN, R. C. LEWONTIN, DAWSON MOHLER, L. B. SLOBODKIN, MONROE STRICKBERGER, E. O. WILSON, and GORDON WYSE for critical help (but not necessarily endorsement) along the way.

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