

THE EFFICIENCY OF THREE METHODS OF SELECTION*

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THE practical value of a plant or animal is almost always affected by several traits. Hence deciding which are the most valuable individuals to select for parents of the next generation forces the breeder to consider several different characteristics. These are not likely all to be equally important or all to be independent of each other. There are many ways of selecting for several different things but these will not often be equally efficient. The most efficient method is that which results in the maximum genetic improvement per unit of time and effort expended.

In planning some of their experimental work, the authors had occasion to compare the theoretical consequences of three fairly simple ways of selecting for net merit, considered as a compound of several different characteristics. While the results are not completely generalized, they are striking enough and seem to be of enough general validity to deserve presenting to plant and animal breeders.

The three methods are designated as the "tandem" method, the "total score" method and the method of "independent culling levels." The "tandem method" is to select for one trait at a time until that is improved; then for a second trait; later for a third, etc.; until finally each has been improved to the desired level. The "total score method" is to select for all the traits simultaneously by using some index of net merit constructed by adding into one figure the credits and penalties given each animal according to the degree of its superiority or inferiority in each trait. In the method of "independent culling levels" a certain level of merit is established for each trait, and all individuals below that level are dis-

carded, regardless of the superiority or inferiority of their other traits.

In order to select most efficiently, the following things need to be known for each trait which influences practical value: (1) The amount by which each unit of variation in it actually raises or lowers an individual's practical value (relative economic value of the trait); (2) the extent to which observed variations in it represent differences in genetic constitution (its heritability); and (3) the genetic and environmental correlations of each trait with the others. The method of total score is most efficient, while the tandem method is the least efficient of the three. The reasons for that and the extent of it will appear in what follows.

Relative Economic Value

Finding the relative economic value of each trait is the first step in framing the ideal toward which the breeder is to strive. This will need to be done separately for each kind of animal or product and may well vary from region to region, or even from farm to farm in the same region, and from one time to another whenever there are relatively permanent shifts in market demands. An example is the finding by Winters² that one pound of wool is worth 3.4 pounds of lamb. In the present article, a with appropriate subscripts will indicate the relative economic values for the different traits. Thus in Winters' example if wool is the first characteristic and lamb is the second, then a_1/a_2 equals 3.4 if both are expressed in pounds.

The efficiency of different methods of selection can be compared by multiplying the improvement expected in each indi-

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vidual trait by its relative economic value. Thus, the *aggregate* genetic gain expected from selection by a given method is

$$\bar{H} = a_1\bar{G}_1 + a_2\bar{G}_2 + \dots + a_n\bar{G}_n \quad (1),$$

where the G 's each represent the amount of genetic improvement expected in that trait.

Heritability

The observed trait (X) is the result of the combined effects of a number (usually large) of genes and of innumerable environmental factors. Let G for each individual be the sum of the *average* effects of all its genes which influence the expression of that trait. G is thus the genetic or breeding value of that individual in that population. Then,

$$X = G + E \quad (2),$$

where E represents the combined effects of all factors which make G and X unlike; that is, differences due to dominance, to epistasis and to environment. For convenience, G , X and E are all expressed as deviations from the population mean. Then from (2), the observed variance (σ^2X) in the population is

$$\sigma^2X = \sigma^2G + \sigma^2E \quad (3),$$

if G and E are uncorrelated, as would be the case unless there is some consistent tendency for better-than-average genotypes to be exposed to better or worse-than-average environment. From (3) we have

$$g^2 = \frac{\sigma^2G}{\sigma^2X} \quad (4),$$

where g^2 represents the heritability or the fraction of the variance in a given trait which is due to the additive effects of genes. Lush¹ discussed methods of estimating heritability in farm livestock.

Selection for one Trait at a Time

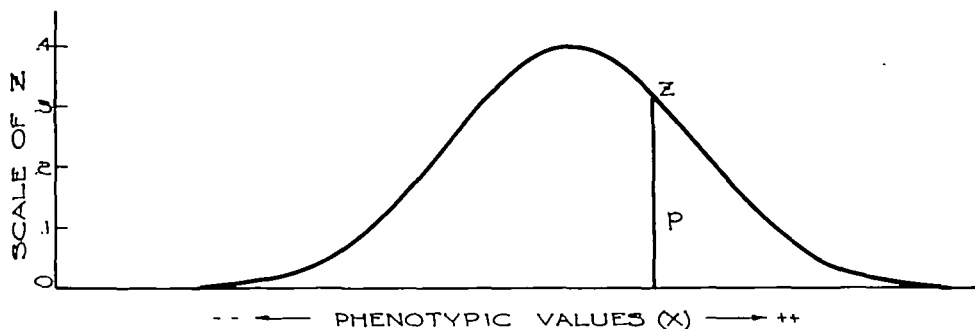
The amount of selection actually practiced is more difficult to measure in herds of domestic animals than in most crop plants because generations overlap, culling is practiced at many ages, etc. To facilitate calculating the intensity of selection, the following simplifications were introduced: (1) Selection is practiced at only one stage of the life cycle; (2) the generations do not overlap; (3) all individuals below a minimum level of desirability are culled without exception; and (4) selected individuals have equal opportunity to leave offspring. Selection under these simplified conditions is illustrated for a normally distributed population in Figure 11.

The genetic gain in the selected group (the genetic average of the selected group minus that of the unselected group, or the phenotypic average of the offspring minus the phenotypic average of the generation in which their parents were born) is expected to be

$$\bar{G} = \frac{z}{p} g^2 \sigma_x \quad (5),$$

where z is the height of the ordinate of the normal curve at the lowest value of X retained.* The proportion which must be saved (p) depends on the reproductive rate and longevity of the species under consideration and upon whether the population is expanding, stationary or declining in numbers. The ordinate (z) of the normal curve is determined by the intensity of selection (p). Values of z for corresponding values of p are given in many statistical reference books. The amount of progress is expected to be larger as p becomes smaller; that is, as selection becomes more intense. The relation is not linear, although it is nearly so from $p = 1.0$ to near $p = .3$. When p becomes less than .3, the amount of progress expected per unit of further decrease in p increases at an ever-in-

*Some additional gain is to be expected if epistatic effects exist, but that is temporary and is not considered further here. Such gains tend to disappear in succeeding generations as the special gene combinations which produced them segregate into others.



SINGLE-TRAIT SELECTION

Figure 11

A normal distribution of phenotypes showing how a population could be separated sharply at a given point into a selected fraction (p) and a remainder which are culled.

creasing rate. The term g^2 appears in equation 5 because it is a measure of the accuracy with which animals having the highest genetic values can be chosen by selecting directly for phenotypes, i.e., of the regression of genetic values on phenotypic values.

In the method of tandem selection, differences in the a values would lead to the most important traits being selected for perhaps three or four generations, while the less important ones would be the object of selection for only one or two generations in each cycle of improvement. In the extremely simple case in which n characteristics were independent and equally important, the *average* improvement per generation in each would be only one n th of the improvement which would be made if it were the sole object of improvement over the entire period.

Selection for a Total Score

The total score method will permit extra merit in one characteristic to offset slight defects in another. By its use individuals with very high merit in one characteristic are saved for breeding even when they are a bit inferior in other characteristics. This does not happen when the method of independent culling levels is used. An example of such a score or selection index is that currently being used in the swine breeding experiments at the Iowa Agricultural Experiment Station for selecting young boars

and gilts. An index (I) is calculated for each pig, based on its own weight at 180 days (W), its score for market desirability at 225 pounds live weight (S) and productivity of its dam (P) as follows:

$$I = .5W - .06S + P.$$

Each pig is given additional credit or penalty for the average weight and score of the litter in which it was born (weighted according to the reliability of the litter average) after litter records are complete.

The greatest practical obstacle to the total score method is the difficulty of knowing how much importance should be given each trait in making up the score. The gain in each trait depends partly upon the heritability of variations in that trait (equation 5) and the aggregate gain is the sum of the products of the gains in individual traits and their relative economic values (equation 1). Evidently, both the heritability and relative economic value of a trait should influence its weight in making up the total score, since both contribute to the aggregate gain. Only one combination of weights allows maximum aggregate gain for a particular set of traits, just as only one combination of regression coefficients allows maximum accuracy in predicting a dependent from a set of independent variables.

If the traits are uncorrelated genetically or environmentally, the correct

weight for each trait in making up the score is in proportion to the product of its economic value and heritability (ag^2). When each of n uncorrelated traits is weighted thus, the aggregate genetic gain is a maximum for any culling level. The aggregate gain expected from selection directly for total score is

$$\bar{H} = \frac{z}{p} \sqrt{a_1^2 g_1^4 \sigma_1^2 + a_2^2 g_2^4 \sigma_2^2 + \dots + a_n^2 g_n^4 \sigma_n^2} \quad (6)$$

In practice, however, some of the traits are likely to be correlated, either because some genes affect two or more traits (pleiotropy) or because the same environmental circumstances affect their developmental processes. Making the weights proportional to ag^2 for each trait is perhaps as good an approximation as can be made until the genetic and environmental correlations are known. But these correlations, if high, may alter the correct weights in an unpredictable manner, just as the regression coefficients in a multiple regression equation (of which general situation this is a particular case) may be changed considerably by the correlation between independent variables.

Independent Culling Levels

When independent culling levels are established for several traits, culling heavily for one trait limits the amount of culling which can be practiced for others. A culling level set too high for a trait which is low in heritability or of small economic importance automatically lowers the intensity of selection which can be practiced for other traits. Only one combination of culling levels, determined by the heritability and economic importance of the traits and by p , the total fraction retained, permits the aggregate genetic gain to be a maximum. For n uncorrelated traits the genetic gain expected from selecting independently for each trait is

$$\bar{H} = a_1 g_1^2 \frac{z_1}{q_1} \sigma_1 + a_2 g_2^2 \frac{z_2}{q_2} \sigma_2 + \dots + a_n g_n^2 \frac{z_n}{q_n} \sigma_n \quad (7)$$

where the q 's refer to the fractions saved for each different trait. In this case,

$$q_1 q_2 \dots q_n = p$$

The product of the relative economic value (a), heritability (g^2) and standard

deviation is a measure of the importance of a trait in the selection program. These values must be known in order to find the culling levels for the various traits which make H a maximum. The procedure of finding the best culling levels for several traits which differ in importance is rather tedious. Different values of q (with corresponding z), subject to the restriction that $q_1 q_2 \dots q_n = p$, are substituted into equation 7 until that combination is found which makes H a maximum.

Table I shows the values of q_1 and q_2 which make H a maximum for certain selected values of p and where the importance of two traits varies. When the traits are equally important (line 1), the same culling level ($q_1 = q_2 = \sqrt{p}$) for each trait is most efficient for every value of p . When one trait is twice as important as the second (line 2), the percentage culled for each trait should be 19 and 1, respectively, if 20 per cent of the total can be culled ($p = .8$); but 76 and 18, respectively, if 80 per cent of the total can be culled ($p = .2$). The relative amount of culling which should be done for the least important character increases as p decreases. However, the two lower lines indicate that even a slight amount of culling for the trait of lesser importance may be too much if the traits differ widely in importance. These figures show vividly the danger of doing real harm to a breeding program by allowing minor points any appreciable weight in selection. This is the real basis for the quarrel between "fancy points" and utility breeding.

Comparison of the Three Methods

The efficiency of the three methods can be compared directly for the special case in which the n traits are independent and the products of the relative economic value, heritability and standard deviation for each trait are equal. Otherwise the formulae remain complex. Under these simplified conditions, the expected genetic gain due to one generation of selection for one trait alone may be written (from equation 5)

$$\bar{H}_1 = ag \frac{z^2}{p} \sigma.$$

That due to selection for a total score based on n traits is (from equation 6)

$$\bar{H}_2 = \sqrt{na}g \frac{z^2}{p} \sigma.$$

For the method of culling levels the expected genetic gain is (from equation 7)

$$\bar{H}_3 = na g \frac{z_3}{q} \sigma,$$

where z_3 is fixed by q , the common culling level for all traits, and $q = n \sqrt{p}$.

The ratio of H_2 to H_1 is \sqrt{n} , indicating that the total score is \sqrt{n} times as efficient as the single trait or tandem method, regardless of the intensity of selection. A geometric analogy may make clearer the reasons for this superiority. In a square the distance from one corner to the opposite one along the sides, is $\sqrt{2}$ times the diagonal connecting the two corners, and in a cube the distance along the three sides is $\sqrt{3}$ times the diagonal connecting opposite corners. That the same principles extend to cases in which more than three characteristics are considered can be visualized by considering each side of the square or cube as being itself a compound score for two or more characteristics. The progress (distance) in any one trait (direction) is

only $\frac{1}{\sqrt{n}}$ times as great by the total score method as if selection were applied for that trait alone. This latter fact is

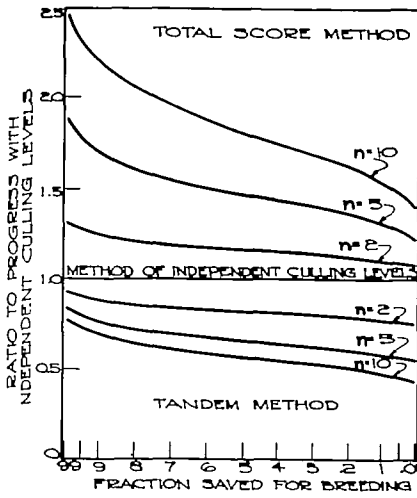
probably the basis for the popular belief that selection is most effective when applied to only one trait at a time.

When the traits differ in their importance but are still independent, the geometric analogy can be extended to rectangles and rectangular prisms with the lengths of the sides proportional to the importance of the traits. The total score method is more than \sqrt{n} times as efficient in those generations when the tandem method is being applied to traits of minor importance and is less than \sqrt{n} times as efficient in those generations when the tandem method is being applied to traits of more than average importance.

The method of independent culling levels is always intermediate in efficiency between the other two if each is compared at the maximum efficiency possible for that method. Figure 12 shows the effect of different values of p upon the relative efficiency of the three methods for two, five and ten equally important, uncorrelated traits. Progress by all three methods is larger with lower values of p but this increase is more rapid under the method of independent culling levels than in the other two; hence the downward trend of the lines indicating relative efficiency of the others. The relative efficiency of the independent culling levels method is closer to that of the tandem method when the selection is very mild, but comes closer to that of the total score method when the selection is very intense. It is a little greater than indi-

TABLE I.—The proportions which should be saved in order to make maximum genetic progress when independent culling levels are used for each of two traits

$\frac{a_1 g^2 \sigma_1}{a_2 g^2 \sigma_2}$	TOTAL FRACTION RETAINED (p)					
	.8		.5		.2	
	q_1	q_2	q_1	q_2	q_1	q_2
1	.89	.89	.71	.71	.45	.45
2	.81	.99	.53	.94	.24	.82
4	.80	1.00	.51	.99	.21	.98
8	.80	1.00	.50	1.00	.20	1.00



METHODS COMPARED

Figure 12

Efficiency of total score method and of tandem method, relative to the method of independent culling levels, where all n of the characteristics are uncorrelated and equally important.

cated in Figure 12 if the traits differ in importance.

The method of independent culling levels has one practical advantage over the total score method in that animals may be culled for each trait whenever that trait becomes evident, without waiting until all the traits can be measured.

Discussion

In all three methods there is always the danger that selection will fall below its maximum efficiency because too much attention is paid to some characteristics and too little to others. In the tandem method that would take the form of selecting first or in too many generations for unimportant things while postponing or selecting too briefly for more important things. In the total score method that would take the form of using too high values of a for some characteristics and too low values for others, or making mistakes in estimating g^2 so that some characteristics would be thought more highly heritable and others less highly

heritable than they actually are; or of failing to consider properly the effects of genetic and environmental correlations between traits. In the method of independent culling levels, the culling level might be set too high for one characteristic, too low for another. The figures in the bottom lines of Table I will show how real this danger is. It cannot be emphasized too strongly that increasing the intensity of culling for one characteristic automatically lowers the intensity of selection possible for other characteristics, if management and reproductive rates remain the same. It is not apparent that one method is more subject to error from this source than the others are; we have not investigated this in detail.

The values of $\frac{s}{p}$ given in statistical

tables are for *normal* curves, whereas biological material is often skewed a little. Skewness is not likely to be important for a characteristic as complicated as net merit. When the population is skewed with the long tail of the distribution toward low merit, progress is faster with mild selection and less rapid with very intense selection than in a truly normal curve. If the long tail of the distribution is toward high merit, the reverse is true—progress is a little less with light selection but a little more with intense selection. The type and extent of skewness found in actual populations seems unlikely to affect seriously the relative efficiency of the three methods.

Selection as actually practiced is usually a combination of the second and third methods except that neither the culling levels nor the score are very definite. Some animals very poor in one or two traits are culled while still young and before their other traits have developed. Some selecting may be done on pedigree, contemporary relatives or progeny. (These may be considered as additional traits in the preceding discussion and formulae.) Finally, the selection process

may be conditioned largely by animal health (which affects p) and by the breeder's ability to measure or observe individual merit for the important traits and to weigh the different traits according to their relative importance. The breeder's carelessness or inability to observe correctly would cause those selected and those culled to overlap somewhat in X , instead of being as distinct as indicated in Figure 11. That would bring the mean of the culled and selected groups closer together so that progress would decrease, apparently as much (relatively) with one method as with another.

The rate of genetic progress may be increased when heritability is low by adopting some criterion of selection other than the individual's phenotype, or by mating systems other than that of random mating of animals selected upon the basis of their phenotypes.⁸ These supplementary methods serve to increase the correlation between the genotype and the criterion of selection, so that fewer errors are made due to the deceiving effects of dominance, epistasis or environmental factors. This leaves the relative efficiency of the three methods unchanged.

Conclusions

Selection for a total score or index of net desirability is much more efficient than selection for one trait at a time. A total score based on n equally important, uncorrelated traits is \sqrt{n} times as efficient as tandem selection for the same traits, one at a time. The progress made in any one trait by the total score method

is only $\frac{1}{\sqrt{n}}$ times as much as if selection were directed at that trait alone.

Selection for several traits by using independent culling levels for each is more efficient than tandem selection for each trait one at a time, the relative efficiency increasing with the number of traits and intensity of culling. Selection on independent culling levels is less efficient than selection on total score but in some cases permits earlier selection without waiting until all traits are mature.

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"FACTS OF LIFE" FOR SOCIOLOGISTS

Another Chapter in the Biological Alice-in-Wonderland

AS the corpus of human knowledge grows more complex, its integration and interpretation becomes increasingly difficult. A point is reached when only a super-genius can do justice to any broadly-based discipline. He must not only have a huge subject-matter at the tips of his mental fingers, but he must also be a master of exposition, if he is to capture the minds of his audience. Super-geniuses are rare enough so that recourse may be had to such makeshifts as the symposium. At its best a symposium contributed to by

the ace minds of a subject can be extremely valuable, as witness such editorial labors of love and erudition as the symposium which summarizes our knowledge of the sex-hormones. But symposia can do more harm than good if the choice of authors is not happy, and if the editor does not succeed in attaining accuracy, continuity and integration. Such difficulties seem to cover the basic failings of a recent ambitious attempt (711 pages) to put sociology on a broad and solid basis.* Many biologists will echo a loud

*PENDELL, ELMER, Editor. *Society Under Analysis*. 21 Cooperating Sociologists. Pp. viii+711. \$4.00. The Jaques Cattell Press, Lancaster, Pa. 1942.