

most recent indicates one aim to emphasize over needs of animal  
genetics and of zoogenetics is to develop methods to breed off the existing  
merits which may be gathered from various sources and breeding  
now to emphasize the same.

## CHAPTER 12

### How Selection Changes a Population—The Outward Results

Although the genes are the units of inheritance, the animal is the smallest unit which can be selected or rejected at any one time. Selection may be between still larger units such as families, inbred lines, breeds, races, etc., but that is optional. The breeder may study the different characteristics of each animal as separately as he will, and may like some of its characteristics very much and dislike others of its characteristics at the same time, but what he *does* with the animal applies to all its characteristics, the admired ones as well as the disliked ones.

The animal is selected or rejected for breeding according to the breeder's opinion of how much its meritorious characteristics outweigh its weaknesses, and in comparison with the other animals which are available for him to use in case this one were rejected. It is thus convenient, when considering the general consequences of selection as the breeder sees them, to consider selection as being made for net merit as if that were a single characteristic. Of course net merit is a compound characteristic affected by many genes, but so too are most measurable characteristics, such as weight, wither height, egg production, litter size, etc. Net merit is also likely to change in definition as economic conditions change, or when one characteristic in the breed improves so much that variations in it become less important than they once were. Also breeders will not entirely agree on the ideal toward which they are striving and on the actual importance of different variations. The yardsticks for measuring net merit are thus somewhat elastic, changing a bit from time to time and from place to place and according to the varied purposes for which the animals are to be used. These are important practical difficulties in measuring net merit for each animal in an objective way so that all would agree on the merit of each animal. Yet the general idea of net merit is as easily understood as the idea of obtaining an individual's net income by subtracting his losses in some enterprises from his gains in the others, or obtaining an individual's net worth in a financial statement by adding his various assets and subtracting his liabilities from them.

Figure 17 shows two diagrams of the way selection might take place. The kind of selection pictured in A corresponds to that actually practiced for important traits in stock breeding where many different traits must be considered. Some animals which are mediocre or even

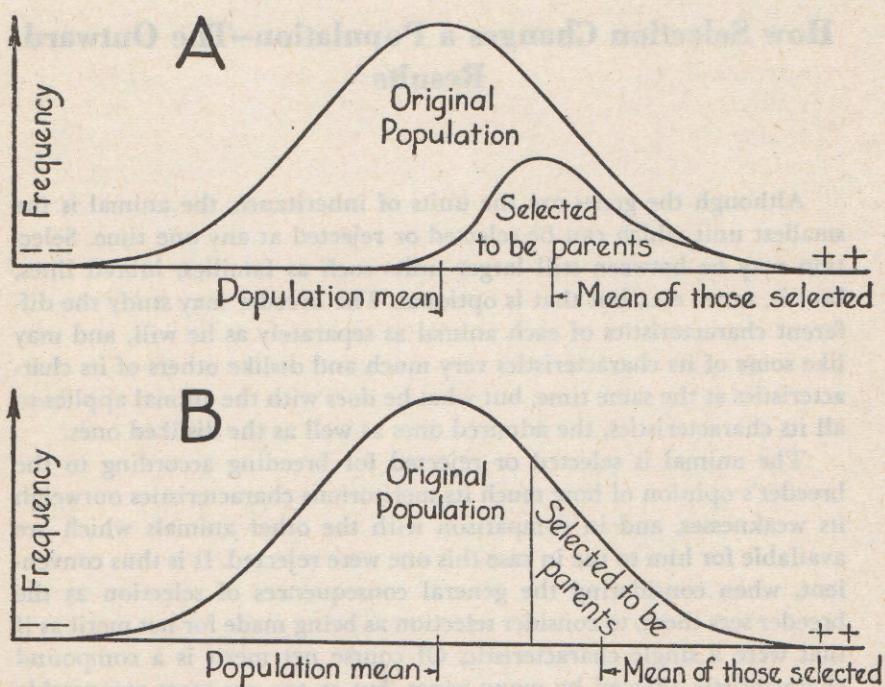


FIG. 17. Two ways in which the merits of those chosen to be parents by rather intense selection might be distributed with respect to the merit of the original population from which they were taken. The better individuals are to the right, the poorer to the left. A indicates the usual kind of selection where at least a few mistakes are made and where some attention must be paid to characteristics other than the one for which merit is indicated here. B is the most extreme form of selection conceivable. No mistakes are made and selection is entirely for the characteristic for which degrees of merit are indicated along the horizontal scale.

inferior in the characteristic pictured are saved because they are unusually desirable in several other characteristics or because the breeder is careless or confused. That pictured in B is the extreme kind of selection which might be practiced in a laboratory experiment on selection for one trait alone, disregarding all others. The selection practiced in livestock breeding can be like that pictured in B, if the net merit of the animal as a whole is the characteristic which is measured along the horizontal axis in B. The kind of selection pictured in B is, of course, more effective if the percentage saved is the same as in A.

## THE SELECTION DIFFERENTIAL

The most useful measure of the intensity of the selection actually practiced is the difference between the average of those selected to be parents and the average of the whole population in which they were born. It is convenient to speak of this superiority of the selected parents as the "selection differential." As a numerical example, if a herd of gilts in their first litters farrow an average of 8.6 pigs and we select for large litter size intensely enough that those which are kept for further breeding averaged 9.5 pigs in the first litters, then the selection differential for litter size at this particular culling was 9.5 minus 8.6 or .9 pig. The selection differential which can be attained is sharply limited by the fact that enough offspring must be saved to replace the parents in any breed stationary in numbers. More than that must be saved in a breed which is increasing in numbers. Reproductive rates and percentages of deaths and other losses from controllable and uncontrollable causes differ among species of farm animals. Table 11 shows what are believed to be

TABLE 11  
ESTIMATED REPLACEMENT RATES WHICH LIMIT BREED IMPROVEMENT

Kind of Animal	Average Interval Between Generations (i.e., Average Age of Parents When Their Offspring Are Born)	Percentage of Progeny Reared Which Are Needed for Replacements in a Population Static in Numbers	
		Females	Males
Horses.....	9 to 13 years	35 to 45	2 to 4
Beef cattle.....	4½ to 5 years	40 to 50	3 to 5
Dairy cattle.....	4 to 4½ years	50 to 65	4 to 6
Sheep.....	4 to 4½ years	45 to 55	2 to 4
Swine.....	About 2½ years	10 to 15	1 to 2
Chickens.....	About 1½ years	10 to 15	½ to 2

reasonable figures for the usual percentage of offspring which must be saved for replacement purposes. The vital statistics of farm animals are not well enough known to make these estimates as accurate as they should be. Of course, there is some variation in the replacement rates from year to year and from farm to farm as conditions of health and management vary.

Table 12 shows for selection such as that pictured in *B* of Figure 17 how much the parents can average above the whole population from which they were selected.<sup>1</sup> It thus gives the maximum selection differ-

<sup>1</sup> Table 12 is for a *normally distributed* population. Most animal breeding populations are nearly enough normal that these figures are sufficiently accurate to be useful. Where a few are culled from the long "tail" of a distinctly skew curve, the gain will be more than is indicated in the upper lines of Table 12, but gains from the heavier culling shown in the bottom lines will be less.

tial which could be attained in a whole breed if the percentage of the population which must be saved for replacement were the only limiting factor. The selection differential in Table 12 is expressed in terms of standard deviations, so as to be applicable to all kinds of characteristics.

An example will show how Tables 11 and 12 are used. The standard deviation of the weights of fleeces shorn in the same year from a group of Rambouillet sheep described in Technical Bulletin 85 of the United

TABLE 12  
SELECTION DIFFERENTIAL (IN TERMS OF STANDARD DEVIATIONS) ATTAINABLE BY VARIOUS  
INTENSITIES OF SELECTION

Percentage of Population Saved	Selection Differential
.90	.20
.80	.35
.70	.50
.60	.64
.50	.80
.40	.97
.30	1.16
.20	1.40
.10	1.75
.05	2.06
.04	2.15
.03	2.27
.02	2.42
.01	2.67

States Department of Agriculture is about 1.86 lbs. (See Table 2 in that bulletin.) If a hitherto unculled group of such ewes and rams were to be culled solely on fleece weight at a single shearing, the 50 per cent of the ewes which it would be necessary to save would excel the flock average by .80 times the standard deviation, or 1.49 pounds of wool. The 3 per cent of the rams with the heaviest fleeces would excel the average for all rams by 2.27 times the standard deviation, or 4.22 pounds of wool. Since inheritance is practically equal from sire and dam, this would make a selection differential of 2.86 pounds of wool at that one shearing, so far as the next generation is concerned.

#### INCREASE TO BE EXPECTED IN THE POPULATION MEAN

The next generation would be expected to be about as variable as the preceding one, but to average outwardly whatever their parents averaged genetically. In case the genes all combined their effects additively and the existing environmental variations did not affect the characteristic at all, the genetic average of the parents would be the same as their phenotypic average, the offspring would average whatever their

selected parents did, and the increase in the population mean per generation would be equal to the selection differential (see Figure 18). Actually the permanent improvement in the population average each generation will be only a fraction of the selection differential. That fraction has for its numerator the additively genetic variance (Chapter 7) and for its denominator the actual variance; i.e., the fraction is

$\frac{\sigma_G^2}{\sigma_G^2 + \sigma_D^2 + \sigma_I^2 + \sigma_E^2}$  which for brevity we may call the "heritability" of the differences which existed in the parental generation before selection began. In addition, epistatic differences will cause temporary gains

which in amount are less than half of  $\frac{\sigma_I^2}{\sigma_G^2 + \sigma_D^2 + \sigma_I^2 + \sigma_E^2}$  of the selection differential. These gains from selecting for epistatic differences tend to disappear in future generations as the genes recombine. They can be maintained only by continued selection.

In the example of selection concentrated on fleece weight, the increase in average fleece weight per generation would be 2.86 pounds per generation in the impossibly extreme case in which all differences in the parental generation were additively genetic, 1.43 pounds per generation in case heritability of differences is 50 per cent, and only .95 pounds per generation in the more probable case that heritability of differences in shearing weights is about one-third. The *annual* increase in the flock average would be about one-fourth or fifth of these increases *per generation*, since the interval between generations, the average age of the parents when the lambs are born, is about four or five years.

This example is somewhat artificial for farm animals in that it assumes that all selection would be practiced at one stage in each generation. Actually, only a few of the rams born would be kept as rams even until the first shearing. Many of the ewes would be culled after the second shearing, others would be culled after the third shearing, others after the fourth, etc., some culling taking place all through the lifetime of that band of sheep and much of the culling being based on things other than fleece weight. All these things operate to lessen the intensity of the culling which could be done at any one time and to render difficult the measurement of the intensity of the selection actually practiced. The example illustrates the general principles that the intensity of selection possible is sharply limited by the necessity for replacements and that the intensity of selection actually practiced is to be measured in terms of the difference between the average of those saved for parents and the average of the generation in which they were born. The method of computing the selection differential in this example is fairly well suited in actual practice to the case of an animal, or some of the

annual plants, where the generations do not overlap and where nearly all the selection is practiced at one stage in the life cycle.

#### CONSEQUENCES OF INCOMPLETE HERITABILITY

Some individuals are mistakenly saved or rejected for parents because the effects of environmental variations make them appear phenotypically better or worse than their genetic values. These environmental effects are not transmitted to their offspring. Selection of the phenotypically superior tends automatically to keep among those saved more than a fair share of those which appeared phenotypically better and less than a fair share of those which appeared phenotypically worse than they were genetically. The environmental effects are left behind when they reproduce. Their genes segregate from these combinations to recombine in the unselected offspring to give a nearly fair picture of the genetic worth of the parents.

Similarly where the favorable genes tend to be dominant the heterozygotes will have been made to appear phenotypically better and the homozygotes relatively worse than corresponds to their average breeding value. The dominance deviations of a parent are not transmitted as such to its offspring, since they are caused by the interaction of a pair of allelic genes and only one gene out of each allelic pair can be transmitted in any one gamete.

Epistatic effects, being dependent on combinations of nonallelic genes, are transmitted to a portion of the offspring, that portion being progressively smaller the more complex the combination. If *A* and *B* are not linked but together have an effect which neither of them has separately, that effect would be transmitted in about one-fourth of the gametes from an *AaBb* individual, whereas the additive effects of *A* would be transmitted in about half of the gametes. An epistatic effect requiring the joint presence of three nonlinked genes, *A*, *B*, and *C*, would be transmitted in only about one-eighth of the gametes from an *AaBbCc* individual, etc. Even when such epistatic effects are transmitted, the gene combinations responsible for them tend to segregate in later generations, this process tending to continue until the genes are combined at random. Hence the partial but transitory gains from selecting for epistatic differences.

Figure 18 shows what would be expected to happen in an experiment on selecting for a perfectly hereditary character, with the selection intensity such that in the high line only the upper half in each generation were saved for parents, while in the low line only the lower half in each generation were saved for parents. Obviously, even with such an impossibly extreme case as perfect heritability (no effects at all by envir-

onment, dominance, or epistasis), it will require several generations of selection before all overlapping between the two lines ceases. Among the offspring of selected parents there will always be some poorer than the poorest of the parents although, if heritability were perfect, the average of the offspring would equal the average of their selected par-

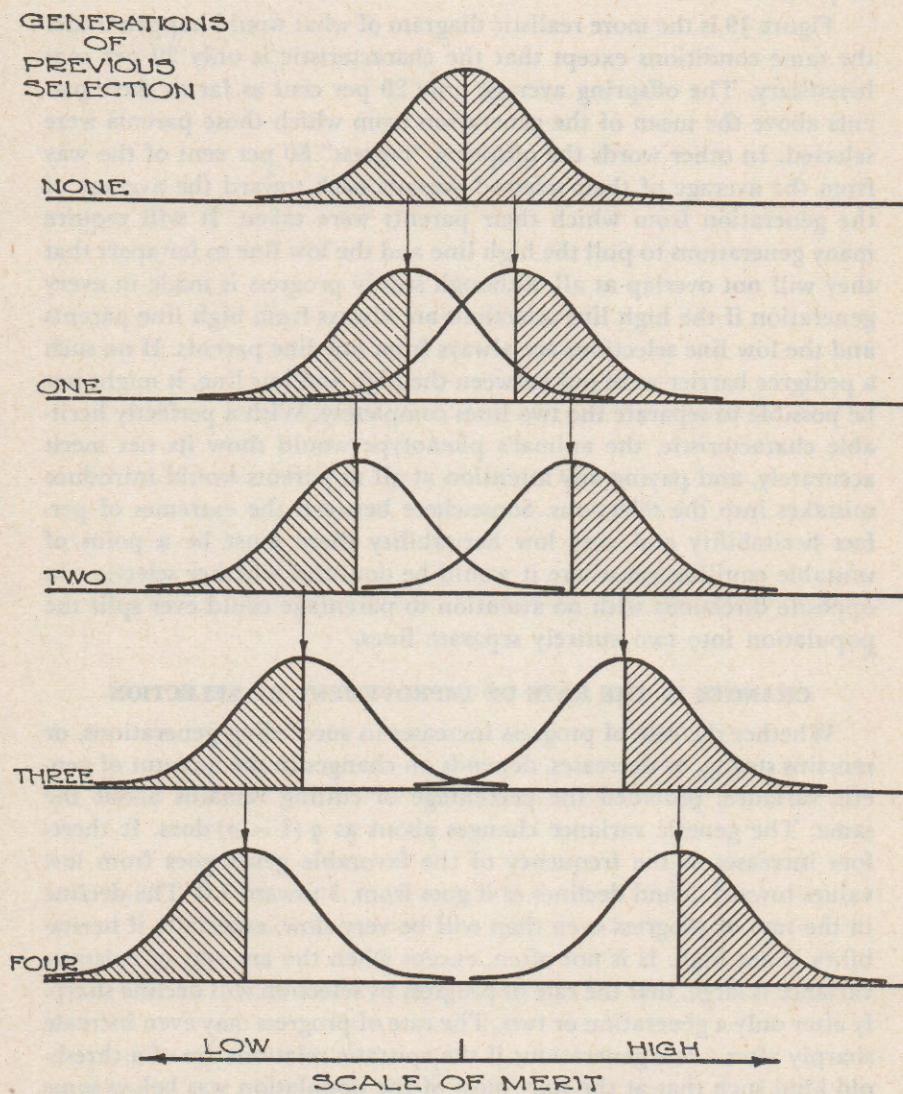


FIG. 18. The results expected when selecting simultaneously a high and a low line for a perfectly hereditary characteristic. In the high line the high half and in the low line the low half in each generation are saved as parents.

ents. The selected parents will not be much more or less homozygous than the average of the population from which they came. They will produce some gametes worse than are typical of them as well as some which are better. When two inferior gametes unite, the result is an offspring poorer than the poorest of those individuals which were saved to be parents.

Figure 19 is the more realistic diagram of what would happen under the same conditions except that the characteristic is only 20 per cent hereditary. The offspring average only 20 per cent as far as their parents above the mean of the generation from which those parents were selected. In other words the offspring "gress" 80 per cent of the way from the average of their selected parents back toward the average of the generation from which their parents were taken. It will require many generations to pull the high line and the low line so far apart that they will not overlap at all, although steady progress is made in every generation if the high line selections are always from high line parents and the low line selections are always from low line parents. If no such a pedigree barrier were put between the high and low line, it might not be possible to separate the two lines completely. With a perfectly heritable characteristic, the animal's phenotype would show its net merit accurately, and paying any attention at all to parents would introduce mistakes into the selections. Somewhere between the extremes of perfect heritability and very low heritability there must be a point of unstable equilibrium where it would be doubtful whether selection in opposite directions with no attention to parentage could ever split the population into two entirely separate lines.

#### CHANGES IN THE RATE OF IMPROVEMENT BY SELECTION

Whether the rate of progress increases in succeeding generations, or remains steady, or decreases, depends on changes in the amount of genetic variance, provided the percentage of culling remains about the same. The genetic variance changes about as  $q(1-q)$  does. It therefore increases as the frequency of the favorable genes goes from low values toward .5 and declines as it goes from .5 toward 1.0. The decline in the rate of progress even then will be very slow, especially if heritability is not high. It is not often, except when the amount of epistatic variance is large, that the rate of progress by selection will decline sharply after only a generation or two. The rate of progress may even increase sharply after a few generations if the epistatic relations are of a threshold kind such that at the start most of the population was below some threshold above which it must rise before the genetic differences could express themselves freely. Something of this kind seems to have hap-

pened in Payne's selection experiments for bristle number in *Drosophila* (Indiana University Studies V, No. 36. 1918) and perhaps in Goodale's selection for body weight in mice (*Journal of Heredity* 29:101-12, 1938.)

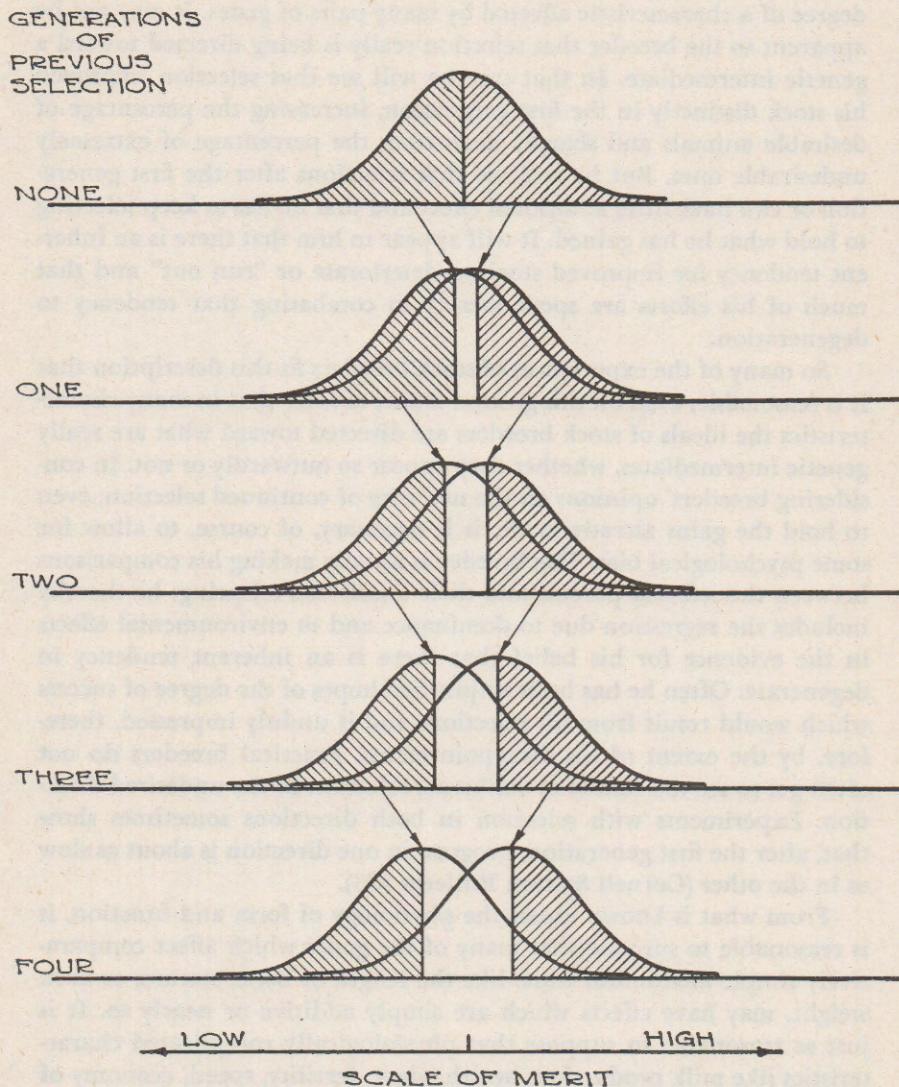


FIG. 19. The results expected when selecting simultaneously a low line and a high line for a characteristic only 20 per cent hereditary. Selection is entirely on the individual's own characteristics except that its parents must have belonged to the same line it did; i.e., there is a pedigree barrier against exchanging animals from one line to the other, no matter what their individual characteristics are. The intensity of selection is such that in each line half are saved to be parents.

**SELECTION FOR EPISTATIC EFFECTS**

The kinds of gene interaction possible are so numerous that they defy cataloguing, but the outward results of selecting for them seem to be typified by what happens when selection favors an intermediate degree of a characteristic affected by many pairs of genes. It may not be apparent to the breeder that selection really is being directed toward a genetic intermediate. In that case he will see that selection improved his stock distinctly in the first generation, increasing the percentage of desirable animals and sharply decreasing the percentage of extremely undesirable ones. But he will see that selections after the first generation or two have little additional effect and that he has to keep selecting to hold what he has gained. It will appear to him that there is an inherent tendency for improved stock to deteriorate or "run out" and that much of his efforts are spent merely in combating that tendency to degeneration.

So many of the experiences of stock breeders fit this description that it is reasonable, even on this ground alone, to infer that in many characteristics the ideals of stock breeders are directed toward what are really genetic intermediates, whether they appear so outwardly or not. In considering breeders' opinions on the necessity of continued selection, even to hold the gains already made, it is necessary, of course, to allow for some psychological bias. The breeder is usually making his comparisons between the *selected* parents and their *unselected* offspring; he thereby includes the regression due to dominance and to environmental effects in the evidence for his belief that there is an inherent tendency to degenerate. Often he has built unjustified hopes of the degree of success which would result from his selections and is unduly impressed, therefore, by the extent of his disappointments. Practical breeders do not often get to see the results of deliberate selection in the undesired direction. Experiments with selection in both directions sometimes show that, after the first generation, progress in one direction is about as slow as in the other (Cornell Station Bulletin 533).

From what is known about the physiology of form and function, it is reasonable to suppose that many of the genes which affect comparatively simple anatomical traits like the length of bone, stature, or even weight, may have effects which are simply additive or nearly so. It is just as reasonable to suppose that physiologically complicated characteristics like milk production, health, vigor, fertility, speed, economy of gain, etc., are dependent for their maximum expression on a harmonious balancing of the magnitudes and functions of many different organs. If that is so, then it must often happen that in selecting for maximum production in these economically important characteristics

the breeder really is selecting for balanced or intermediate sizes of lungs, of heart, of digestive tract, etc. As a purely mechanical illustration, consider how with an automobile the maximum mileage per gallon of gasoline is not obtained at the very slowest speeds and certainly not at the very highest speeds. Moreover the value of the driver's time or the urgency of the errand may make the most desirable speed something other than that which is most economical of gasoline. In most stock judging there is much emphasis on symmetry and "balance" in the animal as a whole. Perhaps this is more justified than would be the case if each gene were consistently desirable or consistently undesirable, as is inferred in many discussions of applied genetics.

A good example of a characteristic which is optimum at an intermediate value is the thickness of the back fat in hog carcasses to be sold in the bacon trade. In Sweden since 1938 the optimum thickness of fat over the middle of the back has been considered to be 29 to 31 mm.<sup>2</sup> When the thickness is already near this optimum, an increase or decrease of one millimeter changes the carcass value only a little. But when the fat is already extremely thin, or much too thick, then one more or one less millimeter in thickness makes a large change in the value of the carcass. For example, an increase of one millimeter would change the carcass score as follows when the initial thickness is as shown:

Initial thickness	Change in score
13 mm.	3.5 points increase
19 mm.	2.2     "     "
27 mm.	.5     "     "
33 mm.	.6     "     decrease
36 mm.	1.3     "     "
44 mm.	3.1     "     "

Thus a gene which will increase backfat thickness one millimeter would be highly desirable in a population where the carcasses range between 14 and 22 millimeters in thickness. Most of its effects in that population would be additive and selection for the relatives of those which have the best carcasses would increase the frequency of that gene. In a population which averages 30 mm. in thickness such a gene would lower desirability of its possessor in about as many cases as it would increase desirability. Its average effect would be zero, all of the individual effects it actually makes would be epistatic, and selection would

<sup>2</sup>For details see: Activities of the research stations for testing swine breeding stock during 1937 (Translated title), Bul. 487 from "Centralanstalten för försöksväsendet på Jordbruksområdet" Stockholm, 1938.

not tend consistently either to increase or decrease its frequency. In a population in which the thickness already ranges from 36 to 44 mm., such a gene would be undesirable, nearly all of its effects would be additive, and selection would tend to lower its frequency.

The emphasis laid on symmetry, balance and proportion in most animal husbandry judging, the physiological and mechanical relations between the functioning of an animal and the dimensions of its parts, the fact that so many chemical reactions in metabolism are of a threshold nature, and similar considerations, indicate that situations in which the intermediate is favored over either extreme are rather common, although there may be some strictly linear relations, too. Probably there are many situations in which the regression of desirability on genotype is curvilinear but the curvature is slight enough within the limits of that population that a straight line comes fairly close to describing the facts and selection would change gene frequency a long way before reaching an optimum or some threshold beyond which further changes in gene frequency would have no effect on average outward desirability.

The idea of a desirable intermediate may be extended, and indeed must be extended, to cover cases where two or more intermediates widely separated on the genetic scale may each be more desirable than the genotypes immediately adjacent to them and yet need not be exactly equal in their own desirability. Desirability for the purposes of the animal breeder (or "fitness," if the problem is being considered from the evolutionary point of view) is such a complex thing that there must be many cases where a certain magnitude of a characteristic fits its possessor better for a certain purpose than magnitudes just a little larger or a little smaller would, and yet a magnitude very distinctly larger or smaller would fit it better for some other purpose or ecological niche. A crude illustration of that is milk production in cattle. There are regions, especially in the corn belt, where both specialized beef production and specialized dairy production can be profitable systems of farming. The most desirable milk production for a cow used in the specialized beef farming is just enough to feed her calf well. More than that would lead to some trouble with spoiled udders, etc. But the peak of desirability in specialized dairy production is far different. There may, of course, be other farms where the physical resources and the aptitudes of the owner make an intermediate milk production most desirable. In that case there might exist, even in the same region, several different peaks of desirability in milk production. Another example is size in horses. In most of the United States there is not much demand for a horse which is too big to be a children's pony but too small to be a

good saddle horse for a grown person. If it were small enough (like the Shetlands) or large enough (like the American Saddle Horse), it might have a high cash value; but, if it is one of the "in-between" kinds, there may be few who will want it. Again, if it were between the ideal for saddle horses used for pleasure and the ideal for cavalry horses, or if it

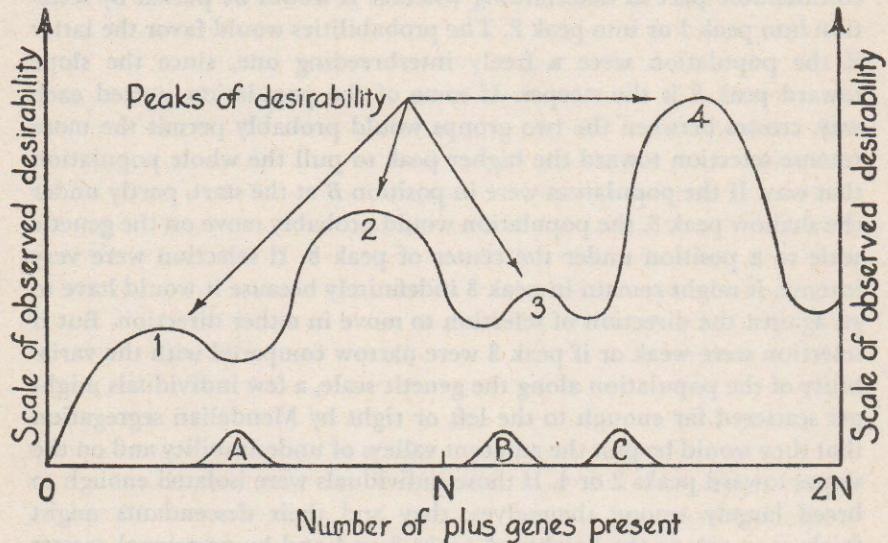


FIG. 20. Illustrating the case of several different genetic intermediates (1, 2, 3, and 4), each of which is more desirable than the genotypes which are most nearly like it. A, B, and C are populations whose averages are at different places along the genetic scale.

were too big for a cavalry horse, it would be at a disadvantage compared with those which were just the right size. Figure 20 shows such a situation diagrammatically, so far as it can be pictured for variation along one dimension.

If the animal's position on the horizontal scale can be seen or measured, the situation offers no new complications over the general case already described for selection directed toward an intermediate. But if only its position on the vertical scale of outward desirability can be observed<sup>3</sup> and the horizontal scale is long enough for the peaks of desirability to be distinctly separated from each other by deep valleys,

<sup>3</sup> Thus, in the example about length of leg and speed in race horses, one might have abundant records on the actual racing speed of many horses but no information at all about the lengths of their legs. Then one would know in detail whether they were fast or slow (their outward desirability) but would know nothing about whether their legs were long or short (their position on the horizontal scale). Two horses might be equally slow, one because its legs were too short and the other because its legs were too long, but a man knowing only the record of speed would not know whether they were alike or far apart on the genetic scale.

then a new kind of complexity occurs. That is shown by *A*, *B*, and *C*, which represent different positions along the genetic scale in which the genotypes of a population might happen to be distributed when selection began. If a population were in position *A*, immediately in the valley of undesirability between peaks 1 and 2, chance would play a considerable part in determining whether it would be pulled by selection into peak 1 or into peak 2. The probabilities would favor the latter if the population were a freely interbreeding one, since the slope toward peak 2 is the steeper. If some of the population started each way, crosses between the two groups would probably permit the more intense selection toward the higher peak to pull the whole population that way. If the population were in position *B* at the start, partly under the shallow peak 3, the population would probably move on the genetic scale to a position under the center of peak 3. If selection were very intense, it might remain in peak 3 indefinitely because it would have to go against the direction of selection to move in either direction. But if selection were weak or if peak 3 were narrow compared with the variability of the population along the genetic scale, a few individuals might get scattered far enough to the left or right by Mendelian segregation that they would be past the adjacent valleys of undesirability and on the slopes toward peaks 2 or 4. If those individuals were isolated enough to breed largely among themselves, they and their descendants might fairly soon rise to the heights of peaks 2 or 4 and by occasional crosses back with the rest of the population might pull the whole population over to their peak. If, however, the occasional individuals which are different from their population in enough genes to be past the valleys interbred freely with the whole population, their offspring would probably be pulled back into the general population because the mates would usually be near the population average.

Whether the population would remain in peak 3 would therefore depend on the balance between selection, the degree to which the population tends to separate into rarely interbreeding groups, and the height and width of peak 3 and the depths of the valleys surrounding it. The more intense the selection, the more the population would tend to be held in that peak. The only force tending actively to get it out of that peak to where it might perhaps find the road to a higher peak is chance at segregation causing gene frequency to vary in a random direction. That is a very weak force in large freely interbreeding populations but may become powerful in a population highly subdivided into small groups which rarely interbreed. This latter condition leads to some mild inbreeding which, under some circumstances, may be necessary to get a population out of a peak where selection has carried it. If the

population were at position *C* when selection began, selection would be almost certain to carry it to peak 4. There would be no need of inbreeding to help in that.

This may explain some of the surprising effects sometimes observed when crossing distinct strains or races. Crossing race *A* and *B* would give a population with gene frequencies putting it nearly in the center of peak 2 and would be considered a "lucky nick." On the other hand, crossing a race already in peak 2 with one already in peak 4 would give a race with gene frequencies which would put it near the much lower peak 3. The unfavorable effect might not show in the first generation of the cross, since each race contributes a full set of its genes, and there is often enough dominance of the favorable genes to furnish a margin of safety. But if the first crosses were interbred, the decline in merit from  $F_1$  to  $F_2$ , when the combinations of genes which worked well together were scattered, might be extreme. How often this actually happens is open to question but it points toward a general principle, valid when epistatic effects are important, that in attempting to perpetuate the good qualities of an individual it should be mated to members of the same race or local strain rather than to equally good individuals from unrelated races where the gene frequencies and combinations may be widely different. This is the principle of "linebreeding" (Chapter 23). Crosses with unrelated or distantly related races may sometimes be advantageous, too, in originating new lines with desirable combinations but should always be considered experimental and venturesome, rather than a dependable general practice.

Desirability for the purposes of the breeder, or fitness in terms of evolution, depends on many different characteristics, each of which may have intermediate peaks of desirability. The interdependence of these on each other's magnitudes increases tremendously the possibilities for such peaks of desirability where all adjacent genotypes which might be reached easily by Mendelian segregation in a freely interbreeding population are less desirable. Figure 20 is a rough sketch of that, showing variability in only one characteristic. Figure 21 shows the interplay of variation in two dimensions on desirability, which is pictured as the height of an irregular surface. By observing the increased complexity of Figure 21 over that of Figure 20, one can imagine how complex the situation may be in reality where adaptation or desirability depends on variation in  $n$  dimensions and  $n$  is a large number!

While it appears impossible ever to know enough about the genes and their physiology and their interplay with environmental circumstances to know a population's position exactly in all  $n$  dimensions of its adaptability, or to explore the surrounding terrain clearly enough to

know whether there is a higher peak of desirability nearby which might be reached, yet the general consequences of selection in such a situation are fairly clear. Selection when first applied will quickly (in terms of generations) carry the population up the steepest slope of increasing desirability to the nearest peak in that direction. Selection cannot carry

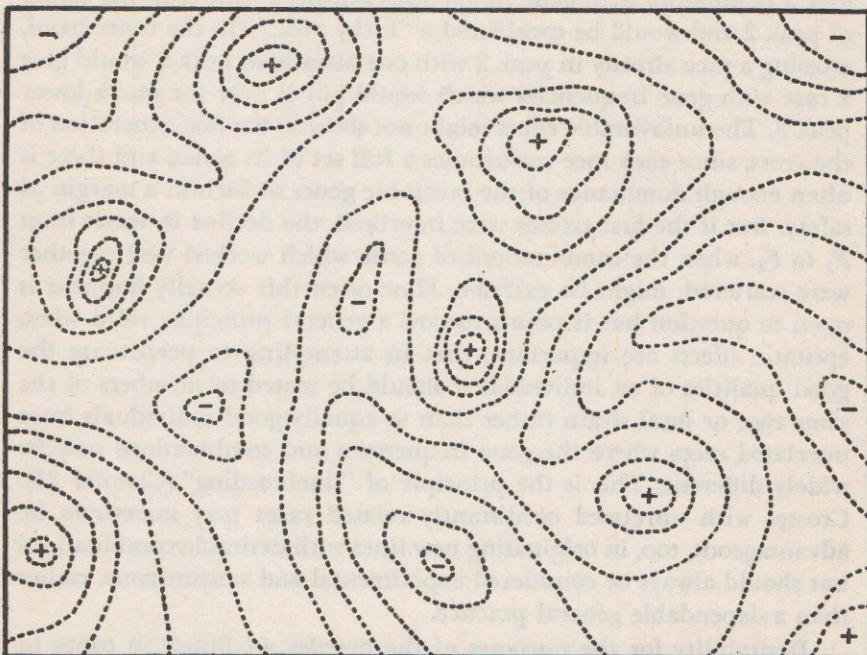


FIG. 21. Contour diagram showing how the level of desirability may depend on genetic variability in two different characteristics. Plus signs indicate peaks, and minus signs indicate hollows. Selection can carry a population up a slope of continuously increasing desirability but cannot carry it down a slope and across an intervening valley to reach a still higher peak (After Wright in *Proc. Sixth Internat. Cong. Genetics*).

the population across a deep intervening valley of lessened desirability to reach a peak of higher desirability on the other side. Only chance wandering of gene frequency against selection can do that, and this chance wandering is a very feeble force except when there is considerable inbreeding. The terrain is apt to be extremely rugged and irregular in places where two or more genes which individually have very minor effects may in certain combinations have extremely important effects on desirability. This gives rise to surprising "nicking" effects which can hardly be seized by selection alone if they are dependent on more than three or four genes which separately have undesirable effects.

As a result of the power of selection to carry populations into these

peaks and its inability to get the population out again, most characteristics which have been under selection for many generations may be expected already to be in some of those peaks. It is only when selection in a new direction is just beginning that the position of the population is as apt to be on a slope ready for rapid progress as it is to be in a peak. As ideals change with economic or other conditions, peaks will sometimes change to valleys or the reverse, thus releasing the population from its peak and permitting rapid progress in some new direction for a time. To some extent this surface of desirability is always changing, like that of the sea, so that the peaks do not remain peaks forever. Yet the rate of such change may perhaps be so slow that, except for changes in ideals which are caused by changes in economic conditions, it should be likened more fairly to geological changes in the heights of mountains and plains.

#### SELECTION FOR MANY CHARACTERISTICS AT ONCE

The practical animal breeder must consider many different characteristics in his selections. Some of these are independent of each other or nearly so; others are positively correlated so that selection for one of them brings with it a little improvement in the other, although, even if  $x$  and  $y$  are correlated rather closely, selection for  $x$  indirectly by selecting for  $y$  is less effective than selecting for  $x$  directly if that is possible. Others are negatively correlated with each other. This makes it a little harder to select for both of them at once than it would be if they were independent. Some characteristics are much more important than others. This needs to be taken into account in balancing excellencies in one respect against deficiencies in other respects when deciding whether to keep or cull the animal. The fact that several things must be considered lowers the intensity of selection possible for each of them, but there is no escape from that so long as all those things have something to do with the net desirability of the animal to the breeder or to his customers.

Culling may be done in at least three general ways. The first or tandem method is to select for one characteristic at a time until that is improved, then for a second characteristic, later for a third, etc., until finally each has been improved to the desired level. The second method is to cull simultaneously but independently for each of the characteristics. This amounts to establishing for each characteristic culling levels, below which all individuals are culled, no matter how good they are in other characteristics. The third method is to establish some kind of a total score or selection index to measure net merit. This would be done by adding the animal's score for its merit in  $x$  to its scores for merit in  $y$ ,

in  $z$ , etc. Then those with the poorest total scores would be culled. Figure 22 illustrates the total score method where two characteristics are involved.

✓ The tandem method is by far the least efficient of the three, even when the characteristics are not affected by any of the same genes and it can be assumed that the improvement made in the first one will not be lost later while selecting for improvement in the others. Selecting for one thing at a time will improve that one thing faster than can be done by any other method of selection, but while that is being done the other things must wait. Where other things must be improved also, the improvement made in the first characteristic while it was under selection must be divided by the whole number of generations necessary to improve them all in order to get the average rate of improvement in that one thing. In the simple case in which  $n$  characteristics are independent and equally important, the average improvement per generation in each will be only one  $n$ th of the improvement which is made in it in the generations when it is the sole object of selection. In this case the selection index method is  $\sqrt{n}$  times as efficient as the tandem method.

The selection index method is more effective than the method of independent culling levels because it permits unusually high merit in one characteristic to make up for slight deficiencies in the other. When culling by the total score method under the simple conditions of  $n$  independent and equally important characteristics, selection for each characteristic will be  $\frac{1}{\sqrt{n}}$  as intense as if all the efforts of selection could have been concentrated on that characteristic alone.

Under the method of independent culling levels, if  $w$  is the fraction of the population which must be saved for breeding, then the intensity of selection for each characteristic is the same as if selection were direct-

ed at that alone but the fraction which must be saved were  $\sqrt[n]{w}$ . For example, if length of body and soundness of feet and legs are uncorrelated in swine, and a breeder must save 10 per cent of his gilts for breeding purposes, he can save the 10 per cent with the very longest bodies if he selects for that alone, or the 10 per cent with the soundest feet and legs if he selects for that alone, but only 1 per cent of his gilts will be in the best 10 per cent in both respects. If he pays equal attention to both things, he must save all gilts which are in the 32 per cent which are longest and are also in the 32 per cent with best feet and legs if he is to save 10 per cent of his gilts altogether. If he takes quality also into account, and if quality is not correlated with body length or with excel-

lence of feet and legs, he will have to save from among the best 46 per cent (instead of 32 per cent) in each trait in order to have 10 per cent of the best in all three respects. Four traits would increase this to 56 per cent instead of 46 per cent. If the traits are positively correlated with each other, the intensity of selection for single traits will not fall off

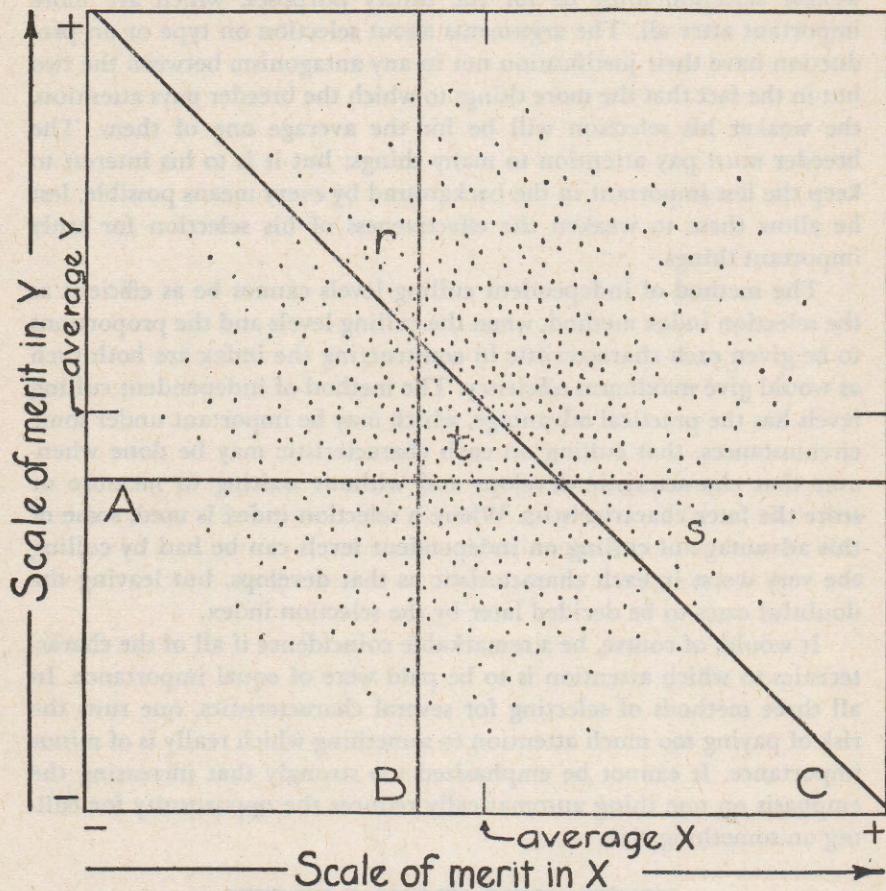


FIG. 22. Superiority of culling on total score as compared with culling independently first for one characteristic and then for another. Each dot represents an individual. Merit in  $x$  is not correlated with merit in  $y$ .  $A$  represents the level of merit in characteristic  $y$  below which all individuals are culled when  $y$  is considered independently. Similarly,  $B$  represents the independent culling level for merit in  $x$ , all individuals to the left of  $B$  being culled.  $C$  represents a level of culling on total score, with  $x$  and  $y$  being regarded as equally important, which would result in keeping an equal fraction of the population. Animals in areas  $r$  and  $s$  would be kept when culling on total score but would be discarded when culling independently on  $x$  and  $y$ , while the reverse would be true of the animals in area  $t$ . The fate of the animals in the other four areas would not be altered by changing the method of culling. If  $x$  and  $y$  were not equally important the example is still valid, but the slope of line  $C$  would be different (Brier et al., pages 153-60, in *Proc. Amer. Soc. An. Prod.* for 1940).

quite so fast with increasing  $n$  as these formulas indicate; but, if the traits are negatively correlated, the intensity of selection for each will fall off a little faster.

Here lies the real damage done by paying attention to "fancy points" in selection; namely, that the more attention given to them, the weaker selection must be for the utility purposes, which are more important after all. The arguments about selection on type or on production have their justification not in any antagonism between the two but in the fact that the more things to which the breeder pays attention, the weaker his selection will be for the average one of them. The breeder *must* pay attention to many things; but it is to his interest to keep the less important in the background by every means possible, lest he allow these to weaken the effectiveness of his selection for truly important things.

The method of independent culling levels cannot be as efficient as the selection index method, when the culling levels and the proportions to be given each characteristic in constructing the index are both such as would give maximum efficiency. The method of independent culling levels has the practical advantage, which may be important under some circumstances, that culling on each characteristic may be done whenever that characteristic develops and without waiting to measure or score the later characteristics. Where a selection index is used, some of this advantage of culling on independent levels can be had by culling the very worst in each characteristic as that develops, but leaving the doubtful cases to be decided later by the selection index.

It would, of course, be a remarkable coincidence if all of the characteristics to which attention is to be paid were of equal importance. In all three methods of selecting for several characteristics, one runs the risk of paying too much attention to something which really is of minor importance. It cannot be emphasized too strongly that increasing the emphasis on one thing automatically reduces the opportunity for culling on something else.

#### CONSTRUCTING SELECTION INDEXES

The principles of constructing selection indexes designed to make maximum improvement, are those of multiple regression where it is desired to predict as accurately as possible an unknown or "dependent" variable from two or more known (independent) variables. In this case the dependent variable is the animal's net genetic merit or breeding value, while its various characteristics or even the characteristics of its relatives are the independent variables.

Four bits of information are needed for each characteristic. 1. The

average amount which a given variation in that characteristic actually raises or lowers the net phenotypic merit of the animal. This we may call the *importance* of the characteristic. 2. The *heritability* of each characteristic is important because it is the average fraction of phenotypic improvement we get in the offspring for each unit of phenotypic merit in the selected parent. 3. *Genetic correlations* between that characteristic and the others may arise if some of the same genes affect two or more of them. These will mean that selection for characteristic  $x$  will help or hinder improvement in characteristic  $y$ , as compared with what would happen if they were independent. 4. *Phenotypic correlations* between that characteristic and the others will exist if some of the same environmental incidents have affected them. This, in combination with differences in heritability, may even lead to some characteristics being useful mainly as indicators of the kind of environment under which more important characteristics developed.

A quantitative example of the idea of relative importance is the finding by Winters (*The Empire Jour. of Exp. Agr.* 8:259-68, 1940) that one pound of wool is worth 3.4 pounds of lamb. The relative importance of each characteristic may need to be established separately for each kind of animal, each region, each type of farming, and almost for each breeder. Naturally this job is never done permanently but needs to be reviewed whenever the market demands and premiums make any large and presumably permanent change. Discussions about what is "the right type" to breed mainly concern the relative importance of different characteristics, although they have in them something of the other three bits of information also.

Heritability can be approximated by doubling the intrasire regression of offspring on their dams. This requires data on several hundred pairs and is not likely to be within the reach of the individual breeder, but from his general observations he can get a rough idea of the relative heritability of two characteristics by observing whether the offspring generally tend to resemble their parents rather closely or slightly in each of these.

The genetic correlation between two characteristics on the same animal can be measured by observing a large number of pairs of closely related animals and correlating characteristic  $x$  in one member of the pair with characteristic  $y$  in the other. This requires large numbers, and the estimates have high sampling errors. It is the bit of information most likely to be lacking when an index is to be constructed.

The environmental correlation between two characteristics can be had by correlating the two characteristics on the same animal and subtracting their genetic correlation obtained as above.

Occasionally it is profitable to pay more attention to a highly hereditary characteristic which is of limited economic importance than to a slightly hereditary one, the variations in which affect the value of the individual animal more strongly. This is because heritability is the fraction which one gets of what he reaches for when selecting the parents, and importance measures the value of that for which he is reaching. One will have more net profit by getting 50 per cent of something which is worth 20 cents than by getting 30 per cent of something which is worth 25 cents! It is a question of deploying the available efforts and resources so as to secure maximum returns.

Because of this relation between heritability and importance, the different characteristics in a selection index should be given emphasis in proportion to their heritability times their importance, rather than in proportion to either one alone. This will be completely true if the characteristics are not correlated. If the characteristics have strong environmental and genetic correlations among themselves, this might alter the size and could even reverse the signs of the attention to be paid to each characteristic when constructing a selection index. This is just a special case of the well-known fact that in a multiple regression equation, strong correlations among the independent variables can alter greatly the net regression coefficients from what they would be if all the independent variables were uncorrelated with each other. Emphasizing each characteristic in proportion to the product of its heritability and its importance is as good an approximation to the proper weights as is possible in most cases.

The few studies yet made seem to indicate that if heritability and importance are known with rough accuracy, the *efficiency* of the index based on them will not be changed much by the intercorrelations between the variables, although the relative importance and even the sign of some of the weights may be changed much. As an example in a swine breeding experiment at the Iowa Agricultural Experiment Station, a selection index was first constructed using only the importance of the items and the observed phenotypic correlation between litter mates. It was:  $I = 1/3 W + S + P + .303 \bar{W} + 1.667 \bar{S}$  where  $W$  is weight at 180 days,  $S$  is score for market desirability,  $P$  is productivity of dam,  $\bar{W}$  is average weight and  $\bar{S}$  is an average score of the litter in which the pig was born. L. N. Hazel's analysis<sup>4</sup> of the data which were then collected in the next few years of the experiment indicated that the most efficient index would have been:

$$I' = .3W - .5S + .5P + .270\bar{W} + .605\bar{S}$$

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<sup>4</sup> *Genetics* 28:476-490. 1943.

The coefficients in the two indexes are markedly different, especially in the reversed sign for the coefficient of  $S$ , yet the efficiency of  $I$  was .364 and that of  $I'$  was .404, which is larger, but not greatly so. By efficiency is meant that progress by selecting exactly according to  $I$  would make progress .364 as fast as could be made by the same percentage of culling if the genotype of every pig were known exactly.

#### SUMMARY OF RESULTS EXPECTED FROM MASS SELECTION FOR NET MERIT

Mass selection is expected to cause the average of each generation to exceed the average of the preceding generation by an amount ( $M$ )

which is equal to the heritability fraction  $\frac{\sigma_d^2}{\sigma_o^2}$  of the selection differential ( $S$ ), the latter being the average merit of those selected to be parents minus the average of the whole generation from which they were taken.

There is also a little deterioration from mutation, but this is too small to be considered further in problems of animal or plant breeding, although it may be important in evolutionary considerations.

When selection is first begun there will also be some temporary gain from epistatic effects. This will be something less than half of  $S \times \frac{\sigma_i^2}{\sigma_a^2 + \sigma_D^2 + \sigma_I^2 + \sigma_E^2}$ . It will tend to disappear with each generation of segregation and recombination and thus, unless constantly renewed by fresh selection, tends to disappear soon after selection is relaxed.

The obstacles to rapid progress naturally fall into two groups: (1) Circumstances or practices which make  $S$  small and (2) circumstances or practices which make  $\sigma_a^2$  small or  $\sigma_D^2$ ,  $\sigma_I^2$ , or  $\sigma_E^2$  large, thereby lowering heritability. Although  $M$  may perhaps be small, it will not be zero, provided both  $S$  and  $\sigma_a^2$  have positive values.

Among things which may make  $S$  small are:

1. Perhaps only a small fraction can be culled. Remedies: Anything which will improve the health of the herd and reduce deaths from disease or accident; earlier breeding and quicker rebreeding of females, and anything else which will increase the number of offspring raised annually per 100 females.
2. The population may be so uniform that the difference between those selected and those rejected cannot be large. Remedy: Sometimes one can change the environment so that genetic differences may express themselves more fully and be magnified. Outcrossing may help.
3. The breeder may be careless about his cullings or changeable in his ideals. This makes the selection more like discarding at random or at least more like the top than the bottom of Figure 17. Remedy: More

care in deciding on the ideals, more attention to detail, planning the cullings and selections well in advance of the time when they must actually be made.

4. The measures or yardsticks of individual merit may not be definite or simple. This has the same effect as 3. Remedy: Clearer and more quantitative definition of goals, more systematic scoring, grading or classifying at regular ages or dates, simple but systematic records of production where possible.

5. The breeder may be trying to pay attention to too many things in his selections, thus weakening the intensity of selection for the more important things. Remedy: Resolutely keeping minor things in the background, perhaps using a selection index.

Among things which make heritability low are:

6.  $\sigma_g^2$  may be small. Remedies: An outcross to a relatively unrelated stock having some desirable characteristics which are absent or rare in the breeder's own herd may restore genetic variability. Probably most breeds of farm animals still have enough genetic variability within them that crossing with other breeds is not necessary for making a large amount of further improvement. Introducing blood from outside the breed cannot be done in most breeds under the prevailing standards of purebreeding, although outcrossing within the breed is always possible. Inbreeding a population without discarding any of the lines tends toward doubling  $\sigma_g^2$  but puts most of it between lines and tends to extinguish genetic variance within lines. When the better lines are selected and the poorer lines are discarded, the genetic variance then remaining is likely to be smaller than was in the population when the inbreeding began. Sometimes it may be possible to alter the environment enough to magnify the outward differences between genetically different individuals, particularly where thresholds are involved, but it may be difficult to find the environmental changes which will do that.

7.  $\sigma_e^2$  is usually large except for a few characteristics such as colors and things which are fairly simple anatomically, such as the dimensions of the bones, shape of head, set of ear, etc. Remedy: Keep the environment alike for all individuals as far as is economical, correct for the effects of the more important differences in environment which did occur, use lifetime averages where those are practicable, and give some attention to the merits of relatives and progeny.

8.  $\sigma_D^2$  may be large. This can be an important obstacle only where most of the undesired genes are recessives already rare, and in pairs of genes where the heterozygote is preferred over both homozygotes. Remedy: Consider the relatives. The collateral ones usually give more help in this respect than the ancestors do. The progeny are still more

informative, especially if they are inbred.

9.  $\sigma_i^2$  may be large. This seems likely to be important only where the population has already been under selection for many generations. Remedy: Consider the relatives and progeny. Inbreed enough to form distinct families, only rarely making crosses between them. Breed within the family as long as its average merit is good.

These ways of overcoming partially the obstacles to progress by mass selection will be considered separately in the following chapters. The purpose of this chapter has been to describe and explain the results of unaided mass selection. It alters the population mean almost in proportion to  $n$  times the amount it changes gene frequency,  $n$  being the number of genes affecting the characteristic.

The rate of improvement per generation may increase or decrease in later generations but is not likely to change rapidly unless there is a considerable amount of epistatic interaction.

Only rarely is mass selection completely ineffective, as when selection is for a heterozygote, when selection has already carried the population into a stable epistatic peak, or when selection is within an entirely homozygous line. Often, however, the rate of progress by mass selection is slow and could be made more rapid by a judicious use of relatives and progeny or by more careful control or consideration of the environment.

#### REFERENCES

The classical cases of selection experiments with higher animals are those of Castle on the hooded pattern in rats, mostly published from about 1914 to 1920, and Pearl's experiments on selection for high egg production in the poultry flock at the Maine Station a little earlier. In plants the Illinois Experiment Station selections for high and low oil content and for high and low protein content in corn kernels and Johannsen's selections in Denmark for seed size in beans are famous among experiments on selection. For brief accounts of these and other actual experimental studies of selection, see:

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## CHAPTER 13

### Aids to Selection—The Use of Lifetime Averages

Many of an animal's important characteristics vary in their expression from one time to another. Familiar examples are: the amount of milk and fat which a cow produces in different lactations, the number of pigs a sow farrows in different litters, the weight of the fleeces which a sheep produces from year to year, the number of eggs a hen lays in different years, the speed with which a horse runs a race, the amount of pull which a draft horse exerts, the degree of fatness of most animals, and many things about an animal's action, temperament, and health. Examples of things which change but little from one time to another are coat color in most farm animals and the dimensions and shapes of bones after maturity is reached.

Most of the variations from one time to another are due to variations in the environment which prevails at the time the observation is made or which did prevail just previously. Internal conditions, such as the temporary state of health, are part of the environment as meant here. So far as the peculiarities of the environment are known and their effects can be estimated, the proper procedure is to correct the animal's production (or score or other figure which is used to represent its appearance or its performance) for the effects of those peculiarities of environment. In this way production records or scores may be "standardized" to what they would probably have been if environmental conditions had been the same as those chosen for standard. It is common practice to correct dairy records for age and for times milked per day. Sometimes they are corrected also for the date at which the next conception occurred, length of preceding dry period, for season of freshening, for weight of the cow, or for the fat percentage of the milk. Likewise, in considering the speed of race horses, allowance is often made for age, for the condition of the track, and for the weight carried. There is almost no limit to the number of such corrections which might be made in cases where many details about the environment or management are recorded. But it is impossible to know all about the environment. Moreover, the correction factors used will not be exactly

correct for every individual, even when they are correct on the average for the whole population. Since it is therefore impossible by the use of correction factors to make all standardized records exactly what they would actually have been under the standard conditions, and since some effort or time is required to use each correction factor, the law of diminishing returns usually makes it scarcely worth while to correct for more than two or three of the most important environmental conditions.

Each standardized record can be considered as equal to the real ability of the animal under the standard conditions plus or minus some error for incomplete or inaccurate correction for conditions which were not standard. If the corrections have been made by a method which on the average is fair for that particular population of records, then the error remaining in any record chosen at random is just as likely to be positive as it is to be negative. The corrected record of the same animal in the next lactation or next year or at the next inspection will be the same real ability of the animal plus or minus another error for incomplete or inaccurate correction to standard environmental conditions. So far as temporary environmental conditions are concerned, these errors remaining in the corrected records will be independent of each other. Hence, if all the records of the animal are averaged together, some of these will have positive errors, and others will have negative errors which will tend to cancel the positive ones. This makes the amount of error in an average less than it is in single records although, of course, it would be too much to expect that the errors would cancel each other *exactly* so that the average would be entirely free of them. The effect of the averaging can be pictured as follows, where  $\pm$  indicates that the error is as apt to be positive as it is to be negative and  $\Sigma$  means "the sum of the":

$$\begin{array}{ll} \text{First observation} & = \text{animal} \pm \text{first error} \\ \text{Second observation} & = \text{animal} \pm \text{second error} \\ \text{Third observation} & = \text{animal} \pm \text{third error} \\ \vdots & \vdots \end{array}$$

$$\begin{array}{ll} \text{Nth observation} & = \text{animal} \pm \text{nth error} \\ \hline \Sigma n \text{ observations} & = n \times \text{animal} \pm \Sigma \text{ errors} \end{array}$$

Dividing by  $n$ , we get:

$$\text{The average observation} = \text{the animal} \pm \frac{\Sigma \text{ errors}}{n}$$

The average of the  $n$  observations differs from the real ability of the animal only by one  $n$ th of the sum of those errors which did not happen to cancel each other. As  $n$  becomes larger, there is more chance for positive and negative errors to cancel. Thus the proportion of error in the average becomes smaller if the errors were really random.

Allowance for the reduced variability of averages must be made when comparing animals which do not each have the same number of records in their averages. For example, let us suppose three cows have the following corrected averages in a herd which averages 400 pounds of fat:

A's only record is 600 pounds.

B has an average of 565 pounds for two lactations.

C has an average of 560 pounds for four lactations.

Which cow probably has the highest and which the lowest real producing ability? The 600 pounds is the highest figure, but this is for a single lactation in which conditions might possibly have been much better than we thought. In other words, it indicates that the cow was a good producer; but we are not sure how much faith it merits. The fact that it is so far above the herd average makes us suspect that its excellence was not due to the cow alone. This cow is somewhat in the position of a prospective employee who bears a letter of very high recommendation, but that letter is written by a man about whose veracity the prospective employer is in doubt! If the records are taken at face value, cow C is the poorest producer of the three; but her record is an average of four different lactations, and it is less likely that she would have had much better environment than we thought in all four of her lactations. Such good luck might have happened to A or perhaps even to B. All three cows in this example are probably high producers, but we need some rule or formula for estimating the real productivity of each if we are to make the least error in estimating which of them is the highest producer, as we might want to do if we were trying to buy one of them or to choose between their sons.

In making such an estimate we need to know something about how "repeatable" these records are. If a cow tends to produce almost exactly the same amount each lactation, just as she is practically the same color every year, the first lactation would tell almost the whole story and would be almost as reliable as the average of four. On the other hand, if dairy records were only slightly repeatable, the first record would be only an indication, not very dependable, and the process of averaging four records would remove much of the error but would also reduce the variability. The measure of repeatability needed is the "coefficient of correlation" between records made by the same cow in this herd of cows. With that coefficient ( $r$  in the following equation) and the herd average and the records of each cow, we can estimate the real productive ability of each cow under the conditions standard in that herd. The equation for this prediction, where the cow's average is based on  $n$  records, each corrected for the known environmental circumstances, is as follows:

Most probable producing ability of the cow =  $\frac{nr}{1 - r + nr} \times (\text{her average record}) + \frac{1 - r}{1 - r + nr} \times (\text{the herd average})$ . Another way to state the same formula is that the most probable producing ability of the cow = the herd average +  $\frac{nr}{1 + (n - 1)r}$  times (her own average minus the herd average). The fraction,  $\frac{nr}{1 + (n - 1)r}$ , shows how much we trust the cow's own average as an indication of her real producing ability. When we know nothing about the cow we can make no better estimate of her producing ability than that she is an average cow of that herd. When she has one record, that gives us an indication of what she will produce in future lactations but, if  $r$  is small, this one indication is not very reliable. So we trust it a little but not very far. When she has two records we trust what they indicate about the cow a little more. As  $n$  increases still more we come nearer and nearer to trusting the cow's average completely. Consequently, we have less and less use for the herd average.

The use of lifetime averages makes selection more efficient simply because it reduces the amount of variation caused by temporary circumstances, and therefore lessens the number of mistakes made. That is shown graphically in Figure 23. Because the heritability fraction increases with  $n$ , the breeder actually gets a larger fraction of what he reaches for in his selections. This advantage is partly offset by the fact that the lessened variation among averages prevents him from reaching so far. The very highest averages are not as high and the very lowest averages are not as low as the highest and the lowest single records, respectively. The net result of the large increase in heritability and the small decrease in the selection differential which can be attained with the same percentage of culling is that progress per generation when

selecting on an average of  $n$  records is  $\sqrt{\frac{n}{1 + (n - 1)r}}$  times as much as if selections were made on only one record per animal. Table 13 shows the values of this fraction for a few selected values of  $n$  and  $r$ . Obviously, the method of averaging many records or observations is most useful and most needed for characteristics for which  $r$  is low. Each additional record contributes less additional information than the preceding one did; therefore, much of the entire usefulness of the method of averaging can be had while  $n$  is still as low or 2 or 3, although each additional record adds something more to the accuracy, especially when  $r$  is very small.

In records of yearly milk and fat production, considering only cows which are in the same herd,  $r$  is usually somewhere between  $1/3$  and

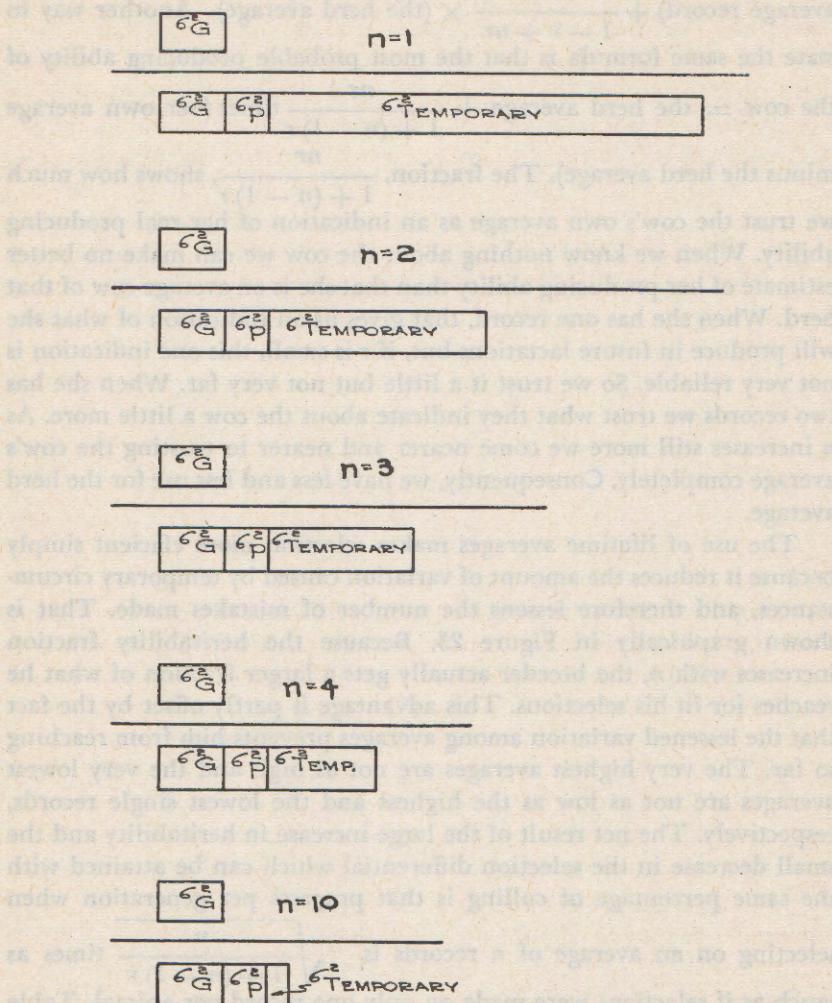


FIG. 23. Diagram showing how the heritability of differences between averages increases as the number ( $n$ ) of records in each average increases. Drawn to scale for the case in which heritability of differences is .12 when  $n$  is 1 and repeatability of single records is .20. That means the case in which 80 per cent of the variance between animals with one record each is caused by temporary environmental circumstances.  $\sigma_G^2$  is the additively genetic variance between individuals.  $\sigma_P^2$  is the variance due to permanent but nontransmissible differences between individuals. These include differences due to dominance deviations, epistatic deviations, and to such effects of environment as are permanent for each animal but differ from one animal to another. As  $n$  increases, the variance due to temporary things falls to one  $n$ th of its value in single records.

1/2. We shall not be far wrong if we take 2/5 as the general figure to be used in the preceding equation, although a higher figure would be justified in herds where management has been unusually standardized and corrections for the known environmental circumstances have been unusually complete. In fact,  $r$  is the fraction of the total variance among the corrected records which is due to permanent differences between cows; and  $1 - r$  is the fraction of the variance caused by temporary circumstances which vary from one record to another of the same cow.

TABLE 13  
PROGRESS WHEN SELECTING BETWEEN ANIMALS WITH  $n$  RECORDS EACH, AS A MULTIPLE OF THE PROGRESS WHICH COULD BE MADE BY SELECTING BETWEEN THEM WHEN THEY HAD ONLY ONE RECORD EACH

n	$r$								
	.1	.2	.3	.4	.5	.6	.7	.8	.9
2.....	1.35	1.29	1.24	1.20	1.15	1.12	1.08	1.05	1.03
3.....	1.58	1.46	1.37	1.29	1.22	1.17	1.12	1.07	1.04
4.....	1.75	1.58	1.45	1.35	1.26	1.20	1.14	1.08	1.04
6.....	2.00	1.73	1.55	1.41	1.31	1.22	1.15	1.10	1.04
10.....	2.29	1.89	1.64	1.47	1.35	1.25	1.17	1.10	1.05

More rigid control of the environment will naturally make  $r$  higher. That is,  $r$  is a description of conditions in a particular population and is not a fundamental biological constant. If we use the fraction 2/5 in the preceding example, the equation simplifies to: The cow's ability =  $\frac{2n}{2n+3} \times (\text{her own average}) + \frac{3}{2n+3} \times (\text{herd average})$ . That gives the following for estimates of the real producing ability of the three cows: A = 480 pounds; B = 494 pounds; C = 516 pounds. C is probably the best and A the poorest of these three, so far as the evidence goes; but all three are good cows, and the differences between them are small enough that we should not be greatly surprised if another lactation or two would change their order.

Figure 24 shows graphically the results of such computations for butterfat production in an actual herd. The numbers along the vertical scale are the barn numbers of the cows. Such a graphic scale of estimated productive ability is a convenient help in making decisions about culling the cows or saving bull calves from various cows. It must be kept reasonably up to date, of course, if it is to be useful. At any particular time some of the cows will have incomplete records which indicate their producing ability but do not merit as much confidence as completed records. In making Figure 24, the records estimated from lacta-

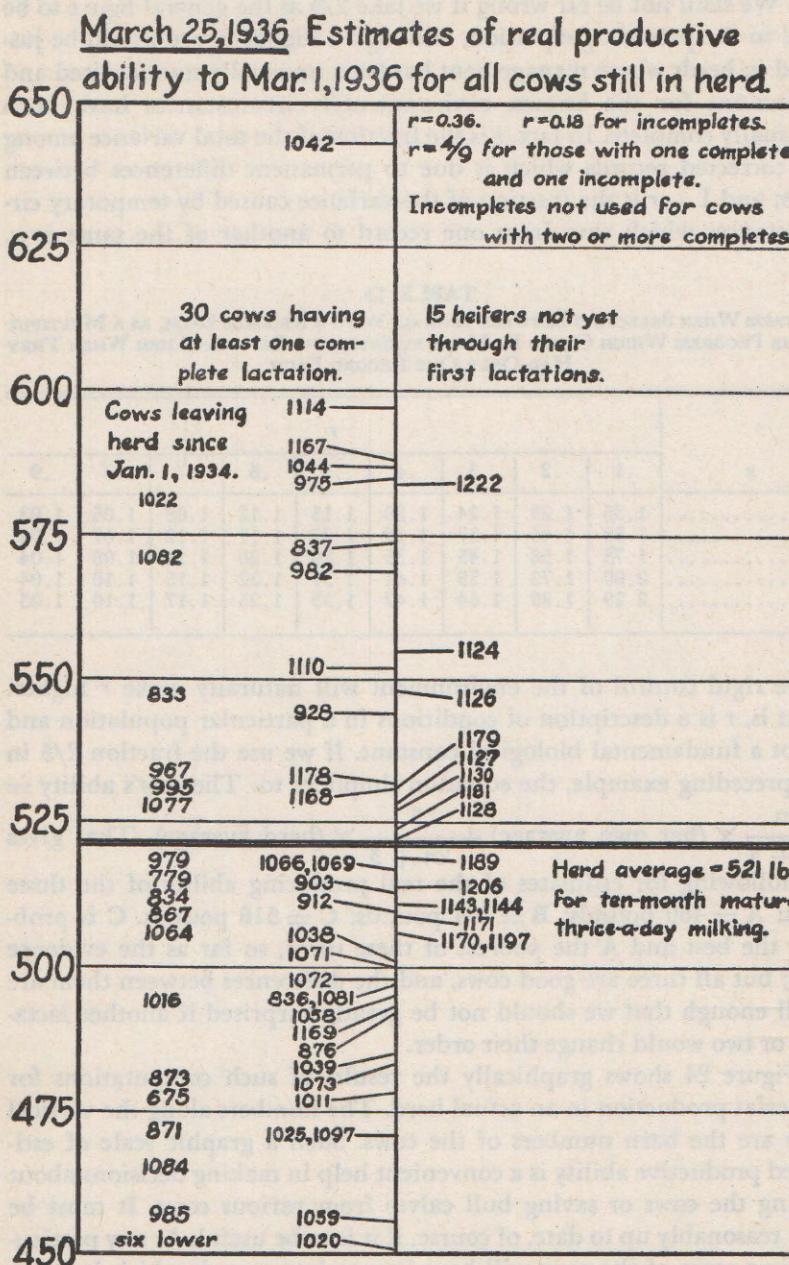


FIG. 24. Estimated producing abilities of many cows with unequal numbers of lactations, based on all information available at the date when the scale was made.

tions still incompletely completed have arbitrarily been given about half as much confidence as completed records in the case of cows which have not yet completed their second record. The incomplete records were not used at all for other cows. The heifers with only an incomplete lactation were placed by themselves on the right to emphasize further the uncertainty about their ability. The cows at the extreme left were included to show whether those which left the herd either through death, disability, or voluntary culling, had really averaged less in productive ability than those which remained.

Many other examples of the use of averages might be given. In each of them it is necessary to know something about the repeatability of the characteristic. In fertility of swine the repeatability of the number of pigs born to the same sow in different litters is about one-sixth. In the weight of fleeces shorn from sheep, the repeatability is about .5 to .6. The corresponding figure for the fleece weights of Angora goats is about .4. Some of the earliest studies on repeatability of production records in farm animals were made on the records of first and second year egg production in egg-laying contests. Most of those figures were of the order of .45 to .60. All of these are computed on the basis of records made within one herd or flock.

The method of averages can be extended to include scores or any other ratings of type which can be expressed numerically. The repeatability of such type ratings is usually low enough that there would be a material gain in the accuracy of selections by obtaining and averaging type ratings of the animal at different times in its life as compared with relying upon the opinion of one judge, no matter how expert, who saw the animal only once. The repeatability of type ratings of dairy cows at intervals of one year was .34 to .55 in the only study<sup>1</sup> yet reported. The opinions which the same judge would hold of the animal if he inspected it at different times in its life usually vary more than do the opinions of several judges who might inspect the animal at nearly the same time. Probably this varies considerably with the class of animal and with the ages at which the inspections are made.

The method of averaging repeated observations, of course, is limited to characteristics which can be observed more than once. It cannot be applied to such things as growth rates, age to sexual maturity, or to carcass qualities which can be observed only upon slaughter of the animals. It is also limited in usefulness for egg production, where such a large part of the total economical lifetime production of the bird is made during its first year.

Of course the costs of waiting to cull until more records are avail-

<sup>1</sup> *Jour. of Dy. Sci.* 25:45-56, 1942.

W. J. G. V.  
8/1/46

able need to be considered, too. Besides the actual loss incurred by keeping any animal which is not actually paying its way, such waiting tends to make the interval between generations longer and thereby to lower the progress *per year*. This will partly offset the gain it makes by increasing the progress *per generation*. The costs of waiting to cull would vary with the animal and with economic circumstances, being higher with hens, for example, where the second year's production is lower than the first, than with cows where the second record is generally some 12 to 15 per cent higher than the first.

In the case of cows the first lactation will be several months along and the heifer may be with calf again before it is certain that the production in her first lactation will be very low. Often it will not cost much then to keep her enough longer for the first three or four months of the second lactation to confirm or disprove what the first lactation indicated. A practical rule for many herds is to cull in their first lactations only those with extremely low production, keeping the moderately low and doubtful ones through the flush of production in their second lactations. They will usually pay at least their feed costs for that, since so much of the production comes in the first half of the lactation.

In many cases the decision to keep or cull must be made while the animals are young if economic loss is to be avoided. For example, with range cattle or sheep the heifer calves and ewe lambs can usually be sold to better advantage and with lower feed costs at or soon after weaning age than if they are kept much longer. The ranchman could cull them more accurately if he could wait until they grow up and until he can have rated their type several times, but the gain from doing this may not be enough to pay for the loss he will take in lower sale prices for those which are finally culled after they are too old to be sold as heifer calves or lambs.

One practical problem involved in using lifetime averages is what to do with records thought to have been made under abnormal conditions for which no satisfactory correction is known. In principle such records should be omitted. The practical difficulty is how to decide fairly when conditions really were abnormal. Some circumstances are definite enough that they offer no difficulty. For example, in Denmark records are omitted for years in which the cow aborted or had foot-and-mouth disease. No other omissions are permitted. Other circumstances are not definite enough to permit a clear decision. For example, a cow may have had a bad attack of milk fever at the beginning of her lactation. The owner may believe that she did not recover soon enough to produce normally during that lactation. But how is one to be certain? To base the decision on the size of the record opens the door to all

kinds of biases. The guiding principle should be to omit no record except when the circumstances are so definite that no doubt can exist. Those circumstances must be something other than the size of the record of performance itself.

Basing selections on lifetime averages will automatically foster some selection for longevity and real "constitution," since breeders will tend to save for sires only the sons of females which have proved themselves by several records of production. When selections are based on lifetime averages, it will hardly be possible for a heifer or gilt with only one record of production to get her son saved to head a purebred herd unless that one record was truly phenomenal.

#### SUMMARY

The use of an average of many repeated observations as a basis of selection is one of the most effective ways of overcoming mistakes and confusion which would otherwise result from the effects of temporary environmental conditions. The method is inexpensive, requiring only the existence of the records, the time needed for averaging them, and whatever it costs to postpone culling until two or more observations have been made. It can be made to foster some selection for longevity and constitution. In using such lifetime averages, allowance must be made for the lessened variability of averages which are based on many records. If this is not done, it will appear that most of the extreme producers, both high and low, are individuals with only one or at most two records. The method is needed most for things which are least constant from one time to another in the animal's life. Much of the gain from using it comes with the second record, but if  $r$  is small the gain from waiting for a third or even a fourth record may be considerable. The method does not help at all to keep the breeder from being deceived by permanent effects of environment, such as permanent stunting when young, nor by the consequences of dominance and complex gene interactions. Placing much reliance on selecting animals by their lifetime averages will naturally lead men generally to buy breeding stock from herds which they know well and in which they have had several opportunities to study the animals.

## CHAPTER 14

### Aids to Selection—Pedigree Estimates

*"The bull gives no milk, of course, yet will not a bull descended from several generations of high-producing dams produce, when mated with a highly productive cow, calves which possess this characteristic to a still higher degree?"—Bergen, in 1780.*

The decision of whether to reject or keep an animal for breeding may be modified by what its relatives are or do. Wherever that is done, the intensity of individual selection is reduced. The average individual merit of those selected must be lowered every time an animal which would be rejected on account of its own individuality is kept for breeding because it has unusually excellent relatives, or every time an individually excellent animal is rejected because its relatives are of low merit.

By paying a reasonable amount of attention to the relatives it may be possible to increase the genetic accuracy of the selections more than enough to offset the decrease in the intensity of selection for individual merit. There is real danger of doing damage by paying too much attention to the relatives, since they are not a perfect guide to the individual's breeding value either. The proper balance between paying too much and paying too little attention to the merits of the relatives shifts from case to case according to how well the merits of the relatives are known, how closely they are related to this animal, how well the individual merit of this animal is known, and how highly hereditary the characteristics are. An understanding of the principles and practical difficulties involved will help in using the approximate rules which in actual practice must guide us in estimating an individual's breeding value from what we know about the merit of its relatives.

From the genetic principles involved, relatives of an individual may all be grouped in two classes: those which are related to it through its parents and those which are its descendants. The former group is considered here collectively under the general term of "pedigree," which is the subject of this chapter, while the latter group will be considered in the next chapter under the term of "progeny test."

Attention to pedigree can make selection more effective only because individual selections are not perfectly accurate. We never know