exactly what genes an individual has. Our knowledge of that is especially scanty when the animal is still immature, as many are when first selections must be made. If we estimate its inheritance from its own appearance or performance, we will make some mistakes on account of the effects of environment, dominance, and complex interactions of genes. If we estimate its inheritance by paying attention to the individuality and performance of its relatives, we may avoid some of those mistakes; but we run the risk of introducing other mistakes, because those relatives will not have exactly the same genes as this animal does. Moreover, our estimate of the genes in those relatives is itself subject to error from our being confused by the effects of dominance, environment, and complex gene interactions on those relatives.

GENERAL PRINCIPLES WHICH LIMIT THE USEFULNESS OF PEDIGREES

The biological basis for the usefulness of pedigrees lies in the fact that an individual gets half of its inheritance from its sire and half from its dam. If we knew what inheritance these parents had, we could estimate what inheritance this individual probably received from them. Because the parents were heterozygous for some of their genes, such estimates cannot be perfectly accurate. Chance at Mendelian segregation plays a part in determining what the parents transmit to any one offspring. An additional limitation on the use of pedigrees is that we will rarely know exactly what genes the parents did have, although we will often know more about their inheritance than about the inheritance of each of the offspring, because the parents have had a longer time in which to demonstrate their characteristics or performance. Also, because some of the ancestors will have had other offspring, they will be to some extent progeny-tested, whereas most individual selections must be made before any progeny are available.

Even if we knew exactly what genes each parent had—and no amount of pedigree study could tell us that much—the sampling nature of inheritance limits the average likeness between the inheritance of an individual and the inheritance of either parent in a random breeding population to a correlation of $+ .50$. On the same basis the correlation between an individual and the average of its two parents is $+ .71$. If much inbreeding, or mating of like to like where ideals are diverse, is being practiced, these correlations will be larger; but in any actual population they will be far from perfect. If we are trying to predict the average merit of many offspring, the effects of chance at segregation will tend to cancel each other. The correlation between the inheritance of one parent and the average kind of inheritance of n of its offspring approaches $+ 1.00$ according to the formula $\sqrt{\frac{n}{n+3}}$ if the other parents of those offspring are a random sample of the breed. The correlation between the average inheritance of both parents and the average inheritance of n of their offspring approaches $+ 1.00$ according to the formula $\sqrt{\frac{n}{n+1}}$.[1] These correlations are between genotypes and not between the directly observable characteristics of the animals, but the formulas explain what seems at first to be a contradiction between the facts that pedigrees cannot be highly accurate for estimating what an individual animal will be and yet can be very accurate in predicting the average qualities of a large number of offspring from one pair of parents.

If we knew exactly what genes the sire and dam each had, nothing would be gained by considering more distant ancestors or collateral relatives. Figure 25 shows a Mendelian example of that with respect to one pair of genes.

- Polled
  - Polled
    - Polled
      - Polled
      - Polled
    - Polled
      - Polled
      - Polled
  - Horned
    - Polled
      - Polled
      - Polled
    - Polled
      - Polled
      - Horned

Fig. 25. A pedigree of a Polled Hereford, illustrating the general principle that study of remote ancestors tells nothing more about an animal's inheritance when the genotype of an intervening ancestor is known with certainty.

Insofar as we are correct in thinking that horned cattle are *pp* and polled cattle are either *PP* or *Pp,* it is certain that the dam in Figure 25 was *pp* and that this offspring of hers is *Pp.* No amount of study of her ancestors would add anything to our knowledge of that. That brings us to the question of how much attention to pay to each ancestor in the general case where we know something about the individual merit of most ancestors but are not entirely sure of the genotype of any of them.

[1] *See also* page 260.

The answer to that question depends on five different circumstances: First, how closely the ancestor is related to the subject of the pedigree; second, how completely the merit of each ancestor is known; third, how well the merit of intervening ancestors is known; fourth, how highly hereditary the characteristic is; fifth, how much environmental correlation there is between ancestor and subject and between different ancestors.

The general fact that an animal gets half of its inheritance from each parent would naturally lead to one form of what is generally called "Galton's law"—of which more is said in chapter 20—namely: In estimating an individual from knowledge about one of its parents, it should be estimated as equal to one-half of that parent plus one-half of the breed average; if it is being estimated from a grandparent, it should be estimated at one-fourth of that grandparent plus three-fourths of the breed average; with a great grandparent, it should be one-eighth of that great grandparent plus seven-eighths of the breed average, etc. The importance of the ancestor in such a prediction equation is halved with each additional generation which intervenes between the individual and its ancestor. This "law" in general is sound in a random breeding population, provided only one ancestor is being considered and provided some conservatism is practiced by basing a smaller share of the estimate on the ancestor and a correspondingly larger share on the breed average wherever the characteristic is not highly hereditary or there is uncertainty that the information about the ancestor really is a true picture of its inheritance. Two ancestors cannot both be used in a single prediction of this kind if one of them is an ancestor of the other. We could combine information about the sire and the maternal grandsire, estimating the animal at one-half of the sire plus one-fourth of the maternal grandsire plus one-fourth of the breed average, with still more emphasis on the breed average as we are less sure that what we know about the sire and grandsire is really typical of their breeding value. But we could not combine information about the sire and the paternal grandsire in the same way because, to a considerable extent, the things which could be estimated from knowledge of the grandsire are the same things which could be estimated better from knowledge of the sire himself. The use of both in a single prediction would be using some of the information a second time.

Czekanowski[2] has explored the question of the comparative importance of sire, grandsire, and great grandsire in the special case when (1) all three are in the same line of descent, (2) no other ancestors are con-

[2] Zeit. f. Ind. Abst. u. Vererbungslehre 64:154–68. 1933.

sidered, (3) exposure of relatives to the same kind of environment has contributed nothing to the correlation between them, and (4) the merits of all three ancestors are equally well known. His figures for the amount of attention (the net regression coefficient) to be given each of these three ancestors for several values of the correlation between parent and offspring are as follows:

	Correlation Between Parent and Offspring						
	.10	.20	.25	.33	.40	.44	.50
Sire	.095	.186	.232	.312	.381	.431	.500
Grandsire	.039	.059	.062	.059	.046	.030	.000
Great grandsire	.016	.020	.018	.012	.006	.002	.000

The figures show how little is to be gained by considering the remote ancestors when the merit of the intervening ones is equally well known. For highly hereditary characteristics the sire's own appearance or performance is almost a perfect guide to the net worth of his inheritance. For slightly hereditary characteristics, relatively more attention should be paid to the remote ancestors, but in that case the predictive value of pedigree is low anyhow, no matter how used. It is doubtful whether Czekanowski's figures have any practical usefulness beyond demonstrating these general principles. In actual practice some ancestors will be much better known than others. For example, if the sire in Czekanowski's problem were still too young for his mature characteristics to be unmistakable or if the grandsire were thoroughly progeny-tested, less attention should be given to the sire and more to the grandsire than these figures indicate.

Collateral relatives in the pedigree are a progeny test which furnishes evidence about the genotypes of their parents or grandparents. Although a grandparent is generally as good an indicator of an individual's inheritance as a half brother or sister, an individual can have only four grandparents but may have a much larger number of half brothers and sisters. In case it does, an estimate of its inheritance based on the appearance and performance of its half brothers and sisters may be much more accurate than an estimate based on its grandparents. The evidence furnished by collateral relatives should be used in the pedigree according to what it shows about the kind of inheritance which the mutual ancestor had and according to the completeness of the evidence. For example, in a dairy pedigree where the production of a large number of paternal half sisters is known, the sire may be considered reasonably well proved, and there is little to be gained by studying his ancestors. If the dam in the same pedigree is still a young cow in her first lactation, considerable information could be gained by considering the maternal grandparents, although consideration of the paternal grandparents would be of little use.

The chief danger in pedigree selection is that it will do more harm by lowering the intensity of individual selection than it does good by making the selection more accurate. Pedigree is not often as accurate a basis for estimating breeding value as individuality is,[3] although it will occasionally be so in a hitherto unselected population, especially if the individuals being selected are still too young to have had much chance to prove their characteristics at the time the selection must be made. Pedigree selection is rarely as useful in animal breeding as it can be at times in plant breeding, because there is almost nothing in animal breeding to correspond to the distinct and uniform lines or families which exist in those plant species, such as wheat and cotton, where self-fertilization or some other intensive form of inbreeding is the rule. In plants in which self-fertilization is possible, an individual may have only one parent, only one grandparent, one great grandparent, etc., and each of these may be more thoroughly progeny-tested than is possible where reproduction must be bi-parental.

PRACTICAL LIMITATIONS ON THE USEFULNESS OF COMMERCIAL PEDIGREES

Often pedigrees contain little information except the names and numbers of the ancestors. To use them at all, you must find from other sources how excellent or poor those ancestors were. That is less true of dairy and poultry pedigrees than of others and is being improved in the pedigrees of most kinds of livestock; but, as printed today, many pedigrees are only a meaningless genealogical jumble of names and numbers to one who does not know from other sources how meritorious those ancestors were. This limitation does not matter much to the man who is thoroughly familiar with his breed. Perhaps all purebred breeders should aim at that goal, but an enormous number of potential customers and even many breeders simply have not time nor opportunity to keep familiar with the merits and deficiencies of the prominent

[3] In a random breeding population in the limiting case most favorable to confidence in the pedigree—the case where the genotypes of sire and dam are perfectly known—the correlation between an animal's breeding value and its own individual appearance or performance is $\sqrt{2a}$ times as large as the correlation between its breeding value and the average genotype of its parents, where a is the additive genetic fraction of the variance in individual appearance or performance. This relation indicates the basis for the general principle that pedigree can become more dependable than individuality for characteristics which are slightly hereditary (i.e., where a is less than 1/2), provided the parents are so thoroughly known that there is little doubt about their genotypes.

breeding animals of their breed. Pedigrees would be more useful to these men if more information were included about the merits of the ancestors, even if that meant only printing the pedigree as far the parents and grandparents. In justice to those who print the pedigrees, it should be emphasized that in most cases there is no information to print because no systematic plan of measuring and recording the merit of individual animals has ever been in operation.

This is no new idea. As long ago as 1832 the following was written in *The Thoroughbred Horse in Prussia:* "If they do not contain production tests, such herdbooks will be useless and without interest, since they would contain only names of which no one knows anything and which mean nothing."

Such information as is given in the pedigrees is usually selected to show the animal in the most favorable light possible. Actual falsehoods in printed pedigrees are rare because of the heavy penalties in loss of business which are exacted of a breeder who is suspected of dishonesty; but plenty of "filler" is still used, although general practice in this respect is improving. An example of "filler" is shown in Figure 26. The information printed under an ancestor's name applies in many cases to half sisters of its parents or grandparents or even to more remote relatives. The following statement was found listed under the paternal grandsire in a pedigree of a bull used in a large dairy herd in Iowa in 1937. "His dam is a granddaughter of that noted transmitter, Sir . . . ., sire of . . . ." The actual records mentioned here were made by cows separated by six Mendelian segregations from the bull in whose pedigree they appeared, and related to him less than 2 per cent. By contrast Figure 27 shows a pedigree in which each bit of information is listed under the ancestor which it most directly concerns.

Generally the ancestors were selected individuals from among their contemporaries. That is especially likely to have been true of the males and hence of their ancestors. Some regression to the breed average is to be expected for that reason, even if the pedigree information is supplied by an utterly impartial and accurate agency. The intensity of the selection practiced in choosing those ancestors is not usually known.

In most pedigrees little information is given about collateral relatives. That is beginning to be remedied in dairy cattle and poultry pedigrees by the inclusion of progeny tests wherever those are available. Occasionally in the pedigrees of meat animals one finds comments on the winnings or performance of brothers or other collateral relatives. Information about collateral relatives may be much more highly selected than information concerning ancestors, since there can be no choosing of ancestors to be mentioned but only selection of data con-

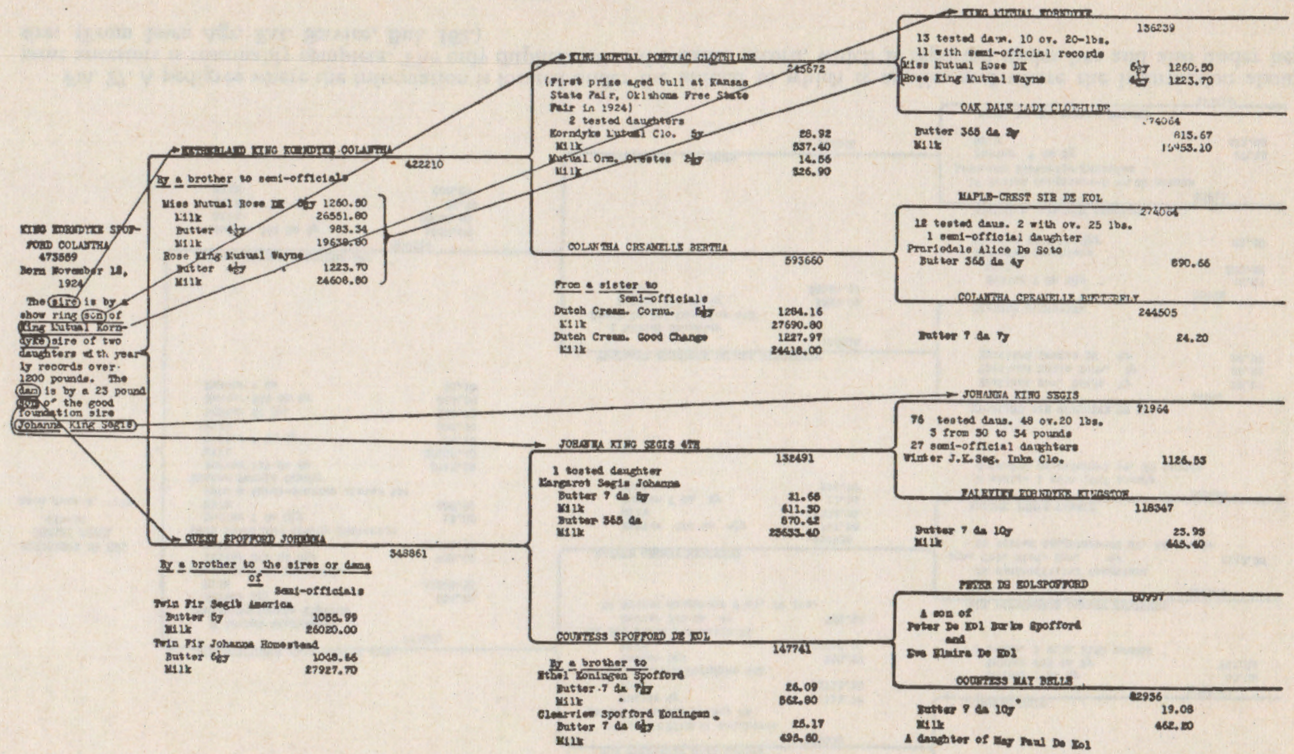

FIG. 26. A pedigree showing a moderate amount of "filler." Favorable items are repeated several times and are placed under animals rather distantly related to those on whose inheritance the items throw most light. (From Iowa Agr. Ext. Service, Bul. 162.)

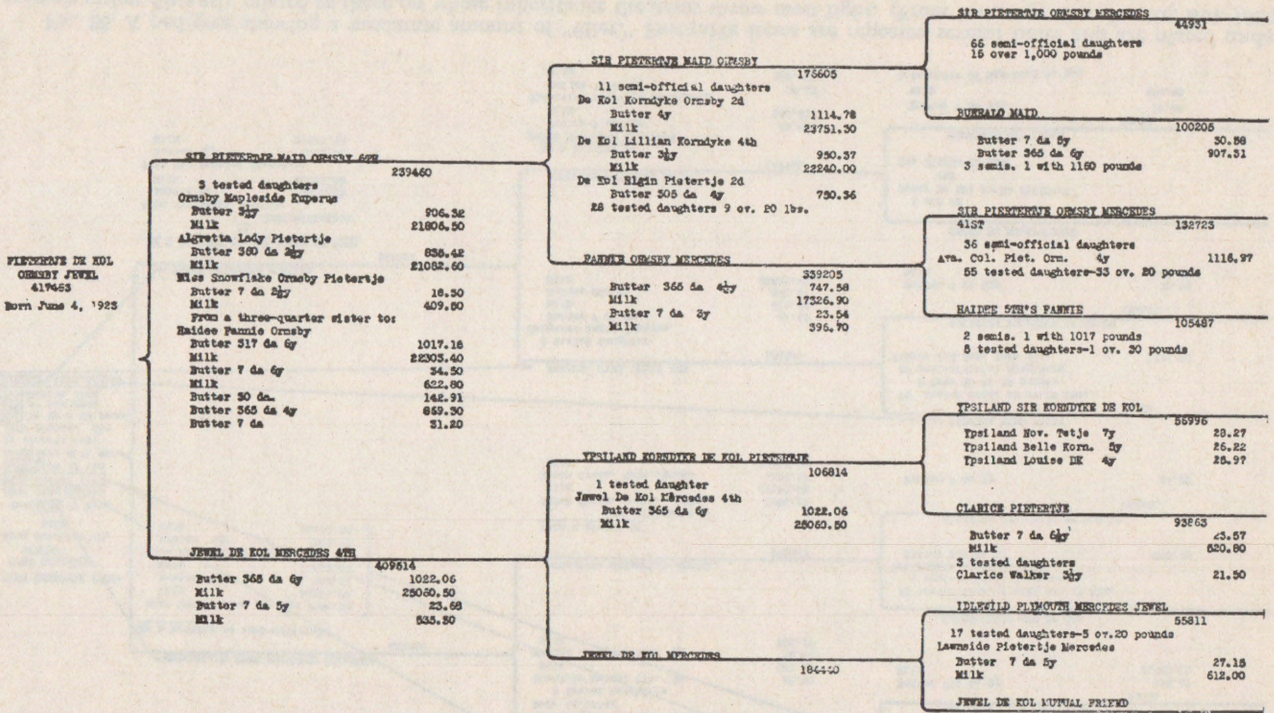

FIG. 27. A pedigree where the information is located under the animal to which it applies and where the information about most ancestors is reasonably complete. The only duplication is the dam's record, which is reported under her and also under her sire. (From Iowa Agr. Ext. Service, Bul. 162.)

cerning them; whereas among the collateral relatives there may be choice of which individuals shall be mentioned and also selection of the best records of those individuals. One often finds in dairy pedigrees such comments as "20 A.R. daughters, two with over 1,000 pounds of fat." Since the records of 18 of the 20 are omitted and the number of daughters not tested is not stated, such a statement tells little more than that this sire was used extensively and was regarded highly enough that 20 of his daughters were tested officially.

Usually no average pedigree of the breed is available for comparison with the one being considered. That lack would not bother the man who has studied enough pedigrees of his chosen breed to get a fairly definite idea of what a typical pedigree is, but many people simply cannot spare the time for such study or do not have access to enough pedigrees to learn what is typical for the breed.

In a sense individual selection is pedigree selection for the next generation. When the parents have been selected for individuality, the offspring which would have had the worst pedigrees are not permitted to be born! Much of the use which might be made of pedigree selection in a hitherto unselected population is simply not available to the breeder who is pursuing the same goal which was pursued by those who bred and selected the parents of his animals. This sets further limits to the usefulness of pedigree selection under ordinary practical circumstances. There are some exceptions to this general situation. One is the fact that fewer males than females are needed for breeding. After the males are born there can be much pedigree selection among them, although there cannot be much among females. This is what a cattle breeder does when he decides he will save a calf from a certain cow if it is a heifer but not if it is a bull. When a breeder's ideals differ distinctly from those of many of his fellows and he lays much importance on things which they consider unimportant and vice versa, the pedigrees of their animals offer him considerable opportunity for selection if he purchases from them. Also, when the ideal of a breed changes, there is momentarily a reappraisal of the merits of the ancestors. While that is happening there is opportunity for pedigree selection on the new basis for a generation or two. Selection among the parents does not reduce the variability among their offspring nearly as much as it does the variability among the parents themselves. Hence in a population which has already been under selection for a generation or two there is much more opportunity for selecting the offspring on their individuality than on their pedigrees.

ERRORS WHICH MAY BE CORRECTED BY PEDIGREE SELECTION

Pedigree selection helps to overcome deception by environment because it does not often happen that the ancestors were all kept under the same environment.

Pedigree study would be of some help in overcoming deception by dominance if full information about the collateral relatives were presented, but that is rarely done. If the recessive is rare and only the direct ancestors are given, pedigree is almost no help in this respect. For example, pedigrees do not help in eliminating red in the black breeds of cattle, since all ancestors are black and the existence of red sibs or aunts or uncles or other collateral relatives is not mentioned. The parents of red calves and something more than half of the sibs of red calves are heterozygotes. Culling them because of their relationship to the red animal would make the genes for red scarcer than can be done by culling the red alone, but present pedigrees do not give the information which would permit that. Nor is it likely that breeders would report such information if it were to be used to reflect unfavorably upon animals they have for sale. Pedigrees help a little in overcoming deceptions by dominance in such cases as the polled Herefords where the distinction between horned and polled is shown in the pedigree.[4]

Pedigree studies may help considerably in overcoming the deceiving effects of complex gene interaction. An unusually good animal from poor or mediocre stock on both sides always suggests that this animal is the result of a lucky combination of several genes all of which are necessary in order to permit each to manifest its desirable effects. The occurrence of such an animal is often called "nicking." In that case the animal would almost certainly be heterozygous for many of the genes whose cooperation is required. There would be small chance of its transmitting enough of those genes in each gamete to cause this excellence to reappear in many of its offspring. Likewise, a poor individual with excellent ancestors and relatives on both sides will be suspected of lacking just a few genes which are necessary for the successful operation of the other genes for the excellent qualities of his family. It will be suspected that he has many good genes which do not manifest their presence in him. If he were used for breeding, many of his mates would transmit to their offspring the necessary genes he lacks. He may be preferred to a better individual from a poorer family, although, of course, he would be discarded if there were enough good individuals in his own family.

RULES FOR THE USE OF PEDIGREES IN SELECTION

In evaluating a pedigree one should estimate what kind of inheritance the sire and the dam had and then average those two estimates.

[4] The probability that a polled calf from polled parents is homozygous for the gene for polledness is equal to $\frac{1 + s + d + sd}{3 + s + d - sd}$ where s is the probability that the sire is homozygous and d is the probability that the dam is homozygous. Probability is expressed on a scale ranging from zero for absolute impossibility to 1.0 for absolute certainty.

Wherever there is uncertainty about an individual's inheritance, conservatism requires that it should be estimated closer to the average of its breed or herd than the evidence about it, if accepted at face value, indicates it to be. Thus, if there is much evidence about the sire but only a little about the dam, the estimate should give much weight to the sire but most of the weight which would have gone to the dam should be placed on the breed or herd average. The estimate of the sire's inheritance, or of the dam's inheritance, is made similarly by averaging the inheritance of its sire or dam and then modifying that average by what its own individual merit seems to be, using the general principle that the individual's own merit should receive more weight than its pedigree under most circumstances. For characteristics which are but slightly hereditary or in cases where the ancestors' merits are much better known than the individual's merit—as, for example, where the ancestors are well progeny-tested or have long lifetime records while the individual is still immature—it may be correct to attach more weight to pedigree than to individual merit.

The more certainly an ancestor's merit is known, the less weight should be placed on its ancestors. This is difficult to place on a quantitative basis, but Czekanowski's table will give a rough idea of about what that relation should be when two ancestors in the same line are equally well known. If the breeding value of the nearer ancestor is known with much more certainty than that of the more remote ancestor, there is scarcely any use to pay attention to the more remote ancestor.

If there is reason to think that much sex-linkage is involved in a particular case, the proper procedure is to give the sire more weight in estimating the inheritance of female offspring and to give the dam more weight in estimating the inheritance of male offspring. (See page 255 for reasons.) The principle of conservatism in cases where the merit of the two parents is not equally known can also give rise to unequal weighting. Thus, in dairy pedigrees where the sire is too young to be progeny-tested but the dam's production is known, much weight can be placed on the dam, but only a little on the sire on account of the uncertainty about the sire's side of the pedigree. In another dairy pedigree where the sire is well progeny-tested but the dam is a young heifer in her first lactation, the situation may be reversed, with more weight being put on the sire's side of the pedigree, only a little on the dam, some on her pedigree, and much on the breed average for conservatism in her case.

Because the ancestors are in most cases selected animals and because the information about them is selected to show them in a favorable light, allowance should be made for regression toward the breed average. There seems to be no quantitative rule for doing that except the general one that the more extreme the selection is believed to have been among the parents or in the information presented concerning them, the more allowance should be made for regression.

SUMMARY

The accuracy of pedigree selection is limited because of the sampling nature of inheritance wherever genes are heterozygous. This makes it impossible to be exactly sure of what an individual offspring will be, even if one were in the extreme position of knowing exactly what inheritance its sire and dam had.

The accuracy of pedigree selection is further limited in practice because one is never entirely sure of the inheritance the parents had, since that, too, must be estimated from their own appearance or performance or from that of various of their relatives.

A limited amount of attention to pedigree will make the selections more accurate, but it necessarily cuts down on the intensity of the individual selection which can be practiced. Too much attention to pedigree may do more harm by decreasing the intensity of individual selection than it will do good by increasing accuracy, since pedigree selection is not perfectly accurate either.

The use of pedigrees is based on the principles: that inheritance is approximately equal from sire and from dam, and that, wherever one's knowledge of the inheritance of the relatives is uncertain, one should be conservative and estimate that the individual is somewhat nearer to the breed average than the performance of its relatives.

Rarely should the pedigree receive as much weight as the animal's own appearance or performance, although that can happen for slightly hereditary characteristics if the merit of parents and grandparents is much better known than the individual's own merit, either because those ancestors are well progeny-tested or because the individual is still too young to show its merits as unmistakably as its parents and grandparents do.

Collateral relatives constitute progeny tests of some ancestor. They therefore make the estimate of its inheritance more certain. If an animal is well progeny-tested, little will be gained by studying the ancestors back of it in the pedigree.

The proper amount of attention to pay to different relatives depends on the closeness of their relationship to the subject of the pedigree, upon how many of them there are, upon how completely the merit of each other relative is known, and upon how highly hereditary the characteristic is.

Because the ancestors are usually selected individuals, some regression toward the breed average is to be expected. Moreover, the information about the ancestors is usually selected to make them appear in the most favorable light. For that reason more regression is to be expected.

Serious defects in the practical use of pedigrees include the fact that the merit of collateral relatives such as sibs, uncles, cousins, etc., is rarely mentioned. If it is mentioned, it usually concerns only certain individuals selected to make the pedigree more attractive and, moreover, is selected information about those.

In most commercial pedigrees, other than those for dairy cattle and poultry, little information of any kind is included except the names and identifying numbers of the animal. Such a pedigree is useful only to the extent that one knows or can find from some other source how meritorious or mediocre those ancestors were.

In a breed which has been selected steadily toward the same goal for two or more generations, there often is only a little room to practice pedigree selection because the worst individuals among those which might have become ancestors were eliminated by individual selection. Therefore, the individuals which might have had the worst pedigrees, if there had been no selection, simply do not get born.

The general conclusion regarding pedigree selection is that it should usually be a minor accessory to individual selection, being permitted to sway the balance in making decisions which are fairly close on individual merit. It is most needed for characteristics which are not very hereditary, for characteristics which only one sex can manifest, and in selections which must be made while the animals are yet too young to show clearly in their own appearance or performance what their individual merit is.

The kind of errors in individual selection which are most likely to be remedied by pedigree selection are those arising from the immaturity of the individual and from mistaking differences caused by environment and epistatic interactions for differences in breeding value. It helps remedy errors caused by dominance when fairly full information about collateral relatives is included, but is not of much help in this respect when only the ancestors are described.

REFERENCES

Marshall, F. R. 1911. Breeding farm animals. pp. 93-104.

Wriedt, Christian. 1930. Heredity in livestock. (Especially the chapter on "Valuation of Pedigree," pp. 168–72. Also pp. 6–10.) New York: The Macmillan Company.

CHAPTER 15

Aids to Selection—Progeny Tests

"The quality of a ram can usually be determined from his conformation and from his get." "You may judge them by their get if their lambs are of good quality."—Varro. The Husbandry of Livestock, the first century B.C.

"One may consider the ancestors as thoroughbred only when all the progeny are thoroughbred."—Thaer, in 1806.

By progeny test is meant estimating the individual's heredity by studying its offspring. The general idea is an old one, as is indicated by Varro's comments some 2,000 years ago. As long ago as 1826 Andre recommended progeny testing as one of the main purposes for keeping herdbooks for sheep. On page 299 in the USDA Yearbook for 1894, the proving of bulls and the continued use of sires of proved excellence are urged.

The principles of the progeny test come from the sampling nature of inheritance. Each offspring receives from the parent a sample half of that parent's inheritance. Each additional offspring receives another independent sample from the same source. If one can find out what was in several such samples, he will be fairly sure of what was in the parent. A crude analogy may make the case clearer. If a barrel contained 100 apples, of which a certain number were ripe while the rest were green, and if we could not get in the barrel to count the apples but could count a sample half of them taken at random, we could tell within certain limits what proportion of the apples in the barrel were ripe. There would be a high degree of uncertainty about our estimate because this one sample might by chance have contained considerably more or less than a fair share of the ripe apples. If the sample half could be placed back in the barrel and thoroughly mixed with the others and then a fresh sample half could be counted and if that process were repeated often enough, we could finally come to the point of knowing how many apples were ripe and how many were green in the whole barrel, although it would take several such samples for us to be sure that we were within three or four of the right number.

The first practical difficulty encountered in using the progeny test is that we do not know exactly what genes the offspring have. We can be deceived by the effects of environment, dominance, and complex interactions of genes in the offspring, just as we could in estimating the parent's genes from its own appearance or performance. There is this important difference, however: There are several of the offspring and the deceiving effects of environment, dominance, and epistasis have an opportunity to cancel each other. Thus, there is a chance for us to know the average inheritance of the offspring with more certainty than we know the inheritance of the parent. The parent is only one individual and in it there has been no chance for the plus and minus errors to have been canceled by averaging.

The second practical difficulty encountered in using the progeny test is that each offspring also has received half of its inheritance from its other parent. Since we usually do not know exactly what was in that parent and will be still farther from knowing just what it contributed to this particular offspring, we are often in doubt as to whether a certain good quality in one offspring came from its sire or from its dam. One way of overcoming this difficulty partially is to use all the available information to estimate the other parent's inheritance; then allow for that according to the general rule that the phenotype of an unselected offspring will tend to average half way between the genetic values of its two parents. Let X represent the unknown genetic value of the parent being progeny-tested and Y be our estimate of the genetic value of the other parent of an offspring which has a phenotype, P. Then the most probable value of P is $\frac{X+Y}{2}$ and the equation, $X = 2P - Y$ furnishes an estimate of X, although not a very dependable one when there is only one offspring, since Mendelian sampling variations, environmental effects, etc., can have made P in a particular case deviate widely from the general rule. Also, of course, we may be rather wide of the mark in our estimate of Y. Another way of overcoming this difficulty consists of progeny-testing an animal by breeding it to a large number of different mates, in the hope that the merits and defects of those other parents would just about cancel each other. Any general difference, then, between the average of the progeny and the average of the breed could be credited to the common parent. This method might, of course, lead to large errors if the other parents were so selected that their average merit was distinctly different from the breed average.

Theoretically, a third way of not being confused by what the other parent transmitted is to use a special "tester strain" so constituted genetically that their contribution to the inheritance of the offspring will not hide the inheritance received from the parent being progeny-tested. Occasionally this can be done in actual practice. Examples are the use of red cows to test the homozygosis of bulls belonging to black breeds, or the use of horned cows to test the homozygosis of polled bulls.[1] This method has its principal use in overcoming the effects of dominance but can also be used to prevent deceit by epistatic effects if the genetics of the situation is known clearly enough that suitable tester animals can be found or produced. Some of the most brilliant research in genetics owes its success to the devising and use of such tester strains. In economic animal breeding, however, this method cannot often be used unless animals already produced for other purposes can be used for testers. The production and maintenance of a suitable tester strain would be expensive, if possible at all. The plan is not practical for females because of the limited number of young they produce and the economic impossibility of using them for several gestation periods to produce to the tester males offspring which would then have to be discarded because of the inheritance from their sire, no matter what they proved about the genotype of their dams. The simplest form of the plan could not be used to test for lethals since there are no tester animals homozygous for those, and it would be difficult to maintain a strain of farm animals heterozygous for a lethal gene. Generally the best that can be done in such a case is to breed the suspected sire to a large number of his own daughters although that requires more offspring than if he could be mated to known heterozygotes.[2] Even where tester animals are available, as in the case of red and horned cattle, it would not be often that the same animals could be used to test for more than a few genes. A sire being progeny-tested for many genes would have to be used on one set of tester animals to test him for some of his genes, on another set to test him for a few more of his genes and on still other sets to provide an adequate progeny test for many pairs of genes, simply because a single strain of animals suitable for testing all genes would not exist. From these and other considerations, it seems likely that the progeny test in actual practice will nearly always have to be made incidentally by studying the offspring produced by mating the sire to the females to which he would be mated anyhow for other reasons.

[1] If a black bull is mated to red cows and produces even one red calf, he is known to be heterozygous. If he produces only black calves, he is probably homozygous, the assurance of that increasing with the number of calves thus produced. The laws of chance governing the case are such that if a heterozygous black bull sires one calf from a red cow, that calf is just as likely as not to be black; but, if he sires two calves, there is only 1 chance in 4 that both will be black; there is 1 chance in 8 that three such calves will all be black, 1 chance in 16 with four calves, 1 chance in 32 with five calves, etc., the chance being $(1/2)^n$ where n is the number of calves sired. Hence, if a black bull has sired more than five or six calves from red cows and none of those calves are red, the chance that such a bull was really heterozygous is exceedingly small.

[2] Berge, S., 1934, *Nordisk Jordbrugsforskning*, pp. 97–114.

It is believed by some, especially in the corn breeding work, that the most accurate tests of the general combining power of different strains can be made by testing them on poor or weak strains rather than on medium or good ones. Theoretically, this seems likely to be true wherever nearly all the favorable genes are completely dominant and the best strains have in them nearly all of those desired genes; or wherever being "best" is largely a matter of having a considerable margin of unused merit, a factor of safety so to speak, which would not ordinarily be needed. Crosses of the various strains to tester material known to be weak in many ways might produce first crosses low enough in average merit to show the differences in reserves or factors of safety among the strains being tested. Such differences would not be detected if the strains being compared were crossed on varieties which were themselves good enough that nearly all the first crosses would be above the threshold below which these extra margins of safety are needed. The practical importance of using poorer-than-average stock for tester strains is uncertain. It is not likely to be as useful with animals as with plants because of the high cost of maintaining tester strains of animals. Attempts to collect tester stocks by selecting poor individuals wherever they are found would encounter practical difficulties in that the supposedly poorer individuals would not be as poor genetically as they are phenotypically. It would be difficult to discount for that correctly.

A third practical difficulty in using the progeny test is that the offspring of a given individual are apt to have been born at somewhere near the same date and to have been reared under much the same environmental conditions. If there was anything unusual about that environment and if proper allowance for that was not made, we will credit or blame the heredity of the parent for something which was really caused by the environment of the offspring. This is probably the most important general limitation on the accuracy of the progeny test, and there seems to be no automatic way of overcoming it. One can merely study as closely as possible the environment under which those offspring were tested and make such allowance as he thinks fairest for any conditions which were not standard.

The principles involved in the progeny test of a sire are illustrated in the equations below. In these equations, "first error of appraisal" includes all mistakes made in correcting the records of "first dam" and of "first offspring" to standard environmental conditions and all mistakes made in allowing for the effects of dominance and epistasis on their records. These equations show how it is that the average error from Mendelian sampling and the average error from mistakes of appraisal become smaller as the number of offspring in the progeny

Law of sampling

dams have either high set of genes or the best set

study

$$\text{1st offspring} = \frac{\text{sire} + \text{first dam}}{2} \pm \text{1st Mendelian error} \pm \text{1st error of appraisal}$$

$$\text{2nd offspring} = \frac{\text{sire} + \text{2nd dam}}{2} \pm \text{2nd Mendelian error} \pm \text{2nd error of appraisal}$$

$$\cdots$$

$$N\text{th offspring} = \frac{\text{sire} + n\text{th dam}}{2} \pm n\text{th Mendelian error} \pm n\text{th error of appraisal}$$

$$\text{Average offspring} = \frac{\text{sire}}{2} + \frac{\Sigma\,\text{dams}}{2n} \pm \frac{\Sigma\,\text{Mendelian errors}}{n} \pm \frac{\Sigma\,\text{errors of appraisal}}{n}$$

$$\text{Sire} = 2 \times (\text{average offspring}) - \text{average dam} \pm 2 \times (\text{average Mendelian error}) \pm 2 \times (\text{average error of appraisal})$$

test increases. They also show why it is important that these individual errors shall be as likely to be plus as they are to be minus. If that is the case, the plus and the minus errors will tend to cancel each other so that their average approaches zero as the number of offspring becomes large. The errors from Mendelian sampling are certain to be thus unbiased, but that may be far from true of the errors in appraising. Because the offspring are apt all to have been reared under similar environment, any peculiarity about that environment for which we have not corrected perfectly is likely to have made most of the uncorrected environmental errors plus or most of them minus. In such a case, the average environmental error does not tend toward zero but toward a figure determined by the kind and size of the systematic error made in standardizing the records. Since such an error is doubled in getting the estimate of the sire and does not tend toward zero as more offspring from the same herd are tested, this is probably the major source of error in most progeny tests—at least if there are enough offspring (more than four or five) to make the errors from Mendelian sampling small. Errors in appraising the effects of environment on the dams can also fail to be random, but this is not so likely to be extreme as in the case of the offspring, since the dams are less likely to have all been kept and tested under the same environment, especially if lifetime records are used for them. Errors in allowing properly for the effects of dominance and epistasis are apt to be more important in the case of the dams than they are in the case of the offspring because the offspring are usually unselected or nearly so, while the dams are often somewhat selected. If dams were selected, considerable regression toward the average of the breed should be allowed in estimating their real breeding value from their records.

It is important that the offspring be an unselected sample. Otherwise the progeny test is biased by the selection practiced in choosing which progeny to include. This bias is difficult to measure and discount. To omit the poor offspring is unfair and misleading.

The result of the progeny test contains a term for the average merit of the dams. If the dams were known to be typical of the breed, that term will be the breed average and, since it will be the same for all sires tested, will not affect the comparison of two sires. If the dams can be assumed to have been a random sample of the breed, only a little error is introduced by ignoring the dams in comparing two sires. If the dams were not a typical or random sample of the breed, then neglect of this term for the average merit of the dams can lead to serious error.

Increasing the number of offspring in the progeny test reduces the errors of Mendelian sampling and the random errors in accordance with the law of diminishing returns. That is, each additional offspring reduces these errors but makes less reduction than the preceding one did, so that further reductions in those errors are slight after the merits of the first few offspring are known. Increasing the number of offspring in the progeny test does *not* reduce the errors from *systematic* mistakes in correcting for environment, dominance, or epistasis. If such systematic errors are large in the population to be studied, little gain in net accuracy is to be had by increasing the number of offspring much past three or four.[3] Additional offspring do contribute some information, but this is so little, compared with the large systematic errors remaining, that efforts to increase still further the number of offspring in the progeny test without first correcting for the systematic errors may be described by the Biblical allusion about straining at a gnat and swallowing a camel.

Requiring too many offspring for proving a sire can actually lower the rate of progress by causing a smaller number of sires to be proved and therefore preventing intense selection among them after they are proved. As a numerical example, if 100 heifers born each year can be used for proving sires, we can prove five sires per year if we require 20 daughters each, ten sires with 10 daughters each or 20 sires with five daughters each. If we must keep for future use the five best among the sires proved each year, we would in the first case have to save them all, regardless of their proof. Nothing would have been accomplished by the proving. In the second case we would need to keep the half which had the best proof. In the third case only the best fourth need be saved. Progress would be fastest in the third case, although the "proof" would be less accurate. On the average the extra errors in the proof would be more than offset by the opportunity to cull more intensely. For maximum progress the optimum number to prove each sire would be about three daughters if selections were entirely on progeny test and if one could neglect the extra costs of maintaining the larger number of bulls

[3] Lush, Jay L., 1931, The number of daughters necessary to prove a sire, *Jour. of Dy. Sci.*, 14:209–20.

while waiting for their proof. The existence of such costs makes the practical optimum number higher, the amount of that shift depending on the costs as well as on how extensively each bull is to be used after he is proved. The essential point here is that it is no use to prove a sire unless something is done on account of that proof—something which would not be done otherwise. Making the proof highly accurate can actually retard progress if it is done at the expense of proving fewer sires, as *must* be the case if the number of daughters required per sire is increased in a cow population of fixed size.

Diallel crossing is a method of progeny-testing introduced into genetic literature by J. Schmidt[4] as a means to avoid setting any value on the dams and to avoid correcting for the environmental circumstances. The breeding values of two males are compared by breeding them at different times to the same females and then comparing the average merit of the two sets of progeny. By referring to the equations used on page 198 to illustrate the principles of the progeny test, it will be seen that if the equation for one sire is subtracted from the equation for another sire, the difference between the real breeding values of the sires will be *twice* the difference between their progeny averages plus or minus terms for differences in the dams, the environments, and the Mendelian sampling errors. Now if the dams are the very same individuals, as they are in diallel crossing, the term for the difference between dams will disappear. If the tests are carried out under the same environmental conditions as, for example, when the two sires are used contemporaneously, half of the females being bred to each sire the first time and then each female being bred to the other sire the next time, then the difference in the environmental conditions approaches zero also. The error from Mendelian sampling can be made small by having a large number of offspring. This leads to the very simple rule that, if this plan can be followed, the difference in the breeding value of two males is simply twice the difference in the average merit of their offspring. The plan has practical difficulties in such cases as dairy cattle, where one can measure production only in daughters and cannot be sure of getting from each cow a daughter by each sire, but it seems to have advantages enough to deserve wider use than it has yet received. It can be extended with more difficulty to the simultaneous comparison of more than two sires. That is being done experimentally with swine[5] but how it will work in practice is not yet certain. The case of four boars requires eight groups of sows which are indicated by letters A to H in the following mating plan:

[4] 1919. Compt. Rend. Lab. Carlsberg, 14, No. 6.

[5] Kudrjawzew, P. N., 1934, Polyallele Kreuzung als Prüfungsmethode für die Leistungsfähigkeit von Zuchtebern. Züchtungskunde, 9 (No. 12) :444–52.

Mating Plan in Polyallel Crossing

	Boar Number			
	1	2	3	4
First season......	A and B	C and D	E and F	G and H
Second season....	H and C	B and E	D and G	F and A

The diallel comparison of boars 1 and 4 is provided by the progeny of sows in groups A and H. The comparison between boars 1 and 2 is provided by the progeny of the sows in groups B and C, etc. There is no direct comparison between boars 1 and 3, but each of these boars is compared directly with boar 2 and also with boar 4. Two indirect comparisons of 1 and 3 are possible from that. The "ring" arrangement provides that, if for any reason the comparison between two boars is not completed, there is still a "chain" arrangement by which any boar may be compared with any other unless there is a second failure in some other comparison.

In an unselected population where individual merit is equally well known for all animals, one offspring is as reliable as a parent in indicating what an animal's inheritance is. But an individual can have only two parents, while there is no such biological limit on the number of offspring it can produce! Because of that, the progeny test can surpass the pedigree as an accurate guide to an individual's inheritance, provided the offspring are half-sibs, and can equal it if they are all full sibs. In an unselected population with the outward merit of each animal equally well known and no environmental correlations between relatives, a progeny test based on three offspring where the other parents can be assumed to have been a random sample of their breed, is equal in accuracy to all that could be learned by studying the animal's pedigree. Two offspring are enough to make the progeny test attain the same level of accuracy if the merits of the other parents are known and discounted. These simple conditions never prevail exactly. Usually the individual merits of the offspring are not as certainly known as the individual merits of the ancestors because the latter are older and have had a longer time in which to manifest their qualities. The offspring are more apt to have been reared and tested under the same environmental conditions which, not being perfectly discounted, are apt to make the progeny test less reliable than under the simple conditions. A circumstance which operates in the opposite direction is that the ancestors were usually selected to some extent, whereas the offspring usually are almost or quite unselected. An extreme example of this effect of selection among the ancestors concerns the occurrence of red in black breeds of cattle. Since all red animals are culled from the pure breed, the pedigree would not be of any help in locating the heterozygous animals (unless perhaps it were one of those few pedigrees which contained information about some red collateral relatives), but the production of even one red offspring would be positive proof of heterozygosis.

These usual exceptions to the simplest theoretical conditions leave the question of when progeny test generally becomes more accurate than pedigree somewhat uncertain in actual practice. Perhaps it is just as well to think of pedigree and progeny test as about equal when there are two or three offspring, although that does not do justice to the usefulness of the progeny test where the ancestors have been highly selected. On the other hand, such a rule does not do justice to the usefulness of pedigree where the offspring have all been raised under some environmental peculiarities about which we do not know or for which our corrections have not been entirely unbiased.

The point at which the progeny test becomes more accurate than the individual merit of the animal itself is of special interest. A numerical solution has been given[6] for the case of a hitherto unselected population where the individual merit of the parent and of each of its offspring are equally well known. In that case at least five offspring are necessary for slightly hereditary characteristics where there is no correlation between the offspring for any other reason than that they are related through this one parent. If the characteristic is highly hereditary, more than five will be necessary. If there is a correlation between the offspring for other reasons, more offspring will be necessary; and if that correlation is as high as + .25, and if correction for it is not made, it will be impossible for the progeny test to become as accurate an indicator of the parent's heredity as the parent's own merit is. In actual practice the parent's individual merit will usually be known better than that of the offspring; but on the other hand, the parents will usually be to some extent the survivors of previous cullings for individual merit and for pedigree. If there has been much selection of that kind, the practical situation is that the possibilities for culling by pedigree or by individuality have been partially exhausted before the progeny test becomes available. The progeny test is thus a fresh opportunity to cull from an entirely new direction. Hence, in a population of selected parents, the progeny test is relatively more useful than the above figures indicate.

Progeny tests are most useful for traits which can be expressed

[6] **Lush, Jay L., 1935, Progeny test and individual performance as indicators of an animal's breeding value, *Jour. of Dy. Sci.,* 18:1–19.**

in only one sex (e.g., milk production, egg production, prolificacy, etc.). In such cases study of the individual animal of the sex which cannot express the trait does little if any good. Selection in that sex is limited to the basis of pedigree and progeny tests, although individual merit is also available as a basis for selection in the other sex.

The fundamental genetic effect of progeny tests is that they permit selections to be more accurate and hence more effective because they prevent the breeder from being deceived as much by the effects of environment, dominance, and epistasis as he might othewise be. They do not alter any genetic process.

All the initial selections must be made while the animals are still young and many of the final selections before they are old enough to have any progeny of known merit. Therefore, the progeny test is applied only to animals which have already met minimum standards of pedigree and individuality. Some loss is incurred by culling without a progeny test some which would have proven to be better genetically than their pedigree or individuality indicated, but it is utterly impossible to test the progeny of them all. The ideal is to select on pedigree and individuality to some extent but not so much that all one's freedom to select will have been exhausted before any of the offspring can be examined. Within limits dictated largely by costs and convenience but partly by the accuracy of selecting on different bases, the breeder should strive to sample enough of those with good pedigrees and individuality that he can still do considerable culling when the results become apparent.

Breeders have always made general but somewhat unsystematic attempts to use the progeny test. They have done this by seeking sires and dams or the sons of sires and dams which had produced unusually good offspring. "Get of sire" and "produce of dam" classes have been included in shows in nearly all countries for many years. In recent years a pronounced interest in progeny testing has developed, especially in dairy cattle and in poultry. In meat animals the widest systematic use of the progeny test has been the Danish system of testing litters of swine[7] which has also been adapted and used widely in Sweden, Canada, The Netherlands, and Germany.

In a certain sense all sires and many dams become progeny-tested eventually, but usually they are dead by that time[8] and the information can be used only in pedigree estimates.

[7] Lush, Jay L., 1936, Genetic aspects of the Danish system of progeny-testing swine, Iowa Agr. Exp. Sta., Res. Bul. 204.

[8] In a survey of the ages of 35,000 dairy bulls in Michigan, it was found that 94 per cent were slaughtered before they reached three years, although a bull cannot be proved before he is five years old. Michigan Quart. Bul. 15 (No. 3) :143. See also Iowa Sta. Bul. 290, *The ages of breeding cattle and the possibilities of using proven sires.*

Where there is sex-linkage, offspring show more about the inheritance of the opposite-sexed parent than they do about the inheritance of the parent of their own sex. This is not often important, but some allowance of that kind can be made where sex-linkage is suspected.

SUMMARY

1. "Progeny test" is a general term for estimating the breeding value of an animal by studying the characteristics of its offspring.

2. The things which may keep the progeny test from being perfectly accurate are: (1) The sampling nature of inheritance makes it possible for the parent to transmit to its offspring inheritance which is better or is worse than is typical of it; (2) the offspring receives half of its inheritance from its other parent, and the breeding value of that other parent may be distinctly different from the average of the breed; (3) environmental effects, dominance deviations, and epistatic deviations may deceive us in our estimate of the real merit of the offspring or of the other parent.

3. Errors coming into the progeny test because of the sampling nature of inheritance may be made as small as we please by getting a sufficiently large number of offspring. Where there are five or more offspring the errors from this source are usually small in comparison with errors from the other sources.

4. Where the other parents can be considered a random sample of the breed or are known to be typical of the breed, errors in the progeny test from neglecting the merit of those other parents are zero or approach zero rapidly as the number of offspring increases. Where the breeding merit of the other parents is distinctly above or below the breed average, allowance for that can best be made by estimating the breeding value of the parent being tested as equal to twice the average merit of its offspring minus the average merit of the other parents of those offspring, with some allowance for regression toward the breed average or herd average.

5. Errors coming into the progeny test through not making fair allowance for environmental conditions which were not standard for the offspring are usually the most serious limitation on the accuracy of the progeny test. Random errors of this kind are reduced rapidly by increasing the number of offspring and thus allowing the plus and the minus errors to cancel each other. Systematic errors are not thus reduced and are likely to be important. The only remedy for this is the general one of studying closely the conditions under which the offspring were reared and tested and making the best allowance one can for those. When errors of this kind are important, not much information is

gained by increasing the number of offspring past three or four.

6. The progeny test can become more accurate than a pedigree estimate in a population as a whole, when there are more than three offspring, but this depends on whether the individual merits of the offspring are as certainly known as the individual merits of the ancestors, on how much environment the offspring have had in common and on how much the variation among the ancestors has already been reduced by selection among them.

7. In a hitherto unselected population, individual merit is usually more dependable than progeny test unless: (1) there are at least 5 offspring, (2) there is no environmental correlation between the offspring, (3) the characteristic is not very highly hereditary, and (4) the individual merits of the offspring are known at least as accurately as the merit of the parent being tested. In actual practice, (2) and (4) are not usually fulfilled, but they may be more than offset by the fact that selection on the basis of pedigree and individuality may already have exhausted much of the possibilities in such selection, while the progeny test comes as a fresh source of evidence from a new direction.

8. Progeny tests are most useful for characteristics which only one sex can express or which, like many carcass characteristics, cannot be measured until the animal is dead.

9. Progeny tests are next most needed for characteristics which are only slightly hereditary and for which individual selection is therefore not very accurate.

10. The chief practical limitation on progeny tests is that they come so late in the animal's life that most of the decisions about culling or using an animal for breeding must already have been made. Therefore, progeny tests have their widest use in making pedigree selections more accurate by pointing to the sires and dams whose offspring are most likely to be worth saving for breeding.

CHAPTER 16

Selective Registration

In nearly all breeds of livestock in the United States every animal which has a registered sire and a registered dam is eligible to registry unless it has one of the few disqualifications which exist in some breeds. Of course, many eligible animals do not get registered; but the decision to register or not to register is left entirely to the breeder. It is occasionally proposed that each animal ought to be inspected and approved by authorized judges or ought to comply with certain minimum standards of production, where those are appropriate, before it is finally accepted for registration. This is selective registration.

This would be a special application of mass selection. No new principles of inheritance are involved. The diagrams in Figure 28 show how various proportions of the population might be affected by such a plan. Diagram *A* shows the impossibly extreme case where the official inspection could be perfectly accurate in eliminating the animals with the lowest breeding values. Diagram *B* shows, with areas of the same size, how the real breeding values might very well be distributed in the case where individual merit is only moderately correlated with breeding value. Some of those which would be eliminated by selective registration would be superior to some of those which would be accepted. That is inevitable wherever outward individual merit is not perfectly correlated with breeding value. The proportions of the different areas in these diagrams are not particularly important. Those vary from breed to breed and from time to time and are different for males and females.[1]

Both diagrams indicate that the animals not now registered include many which are of higher breeding value than some of those which are registered. It is probable that the average breeding worth of those registered is higher than the average breeding worth of the eligible ones which do not get registered, although the difference may not be as extreme as is pictured here. Selective registration would increase the intensity of selection for those genes which would usually make their possessors appear more desirable to the inspectors. This would increase

[1] In the cattle breeds the number of males registered in recent years has generally been about one-half to one-third as large as the number of females registered.

slightly the rate of improvement in the breed, as far as mass selection can do that and as far as the ideals set up to guide the inspectors are in agreement with real merit. Whether the amount thus gained would be sufficient to make selective registration worth the money and effort it would cost is open to some doubt.

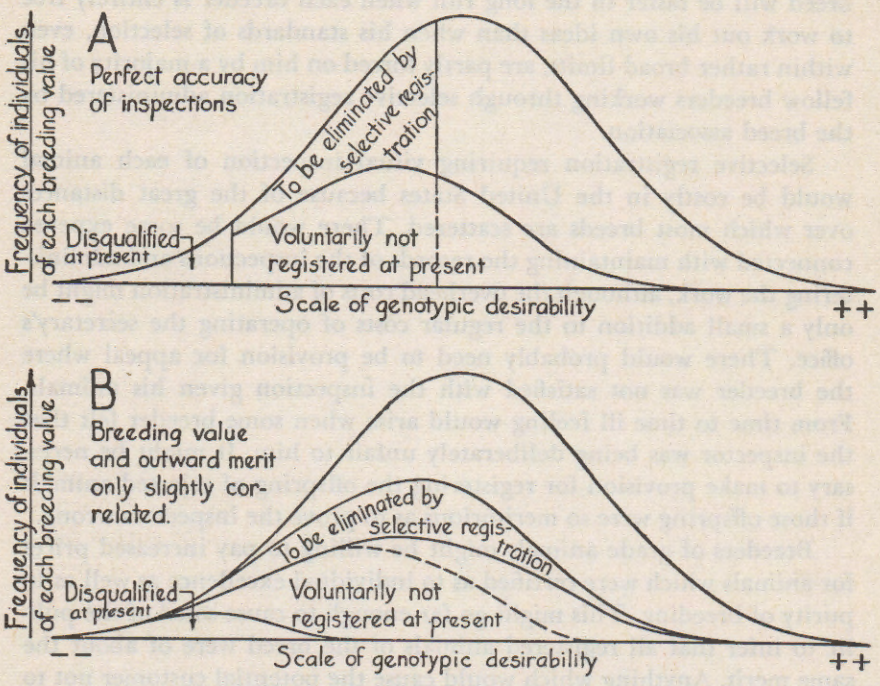

FIG. 28. How the distribution of a population might be affected by selective registration. Corresponding areas are the same size in the two diagrams. The areas in each diagram are exclusive of each other. *A* presents the impossibly extreme case where the inspections could be perfectly accurate. *B* presents a more probable situation where many mistakes would be made by the inspectors although they would be right oftener than they would be wrong. If many were eliminated by the inspectors, it might be necessary to register some of those voluntarily not registered at present. Those would come from the areas just to the right of the dotted lines.

Selective registration would have some tendency to unify the standards of selection within each breed, since each breeder would have to be guided in part by the ideals of the inspectors. Those might not always be superior to his own. This control over standards of selection might do actual harm by preventing individual breeders from trying out their own ideas as freely as they would like. To understand that, one has only to imagine what would have happened if there had been an official system of inspection in the Shorthorn breed when the Cruickshanks were founding the "Scotch" type or in the Poland-China breed when Peter Mouw was forming the "big type." The help which the inspectors would give many breeders in their selections might more than offset this. Moreover, the inspectors would probably be lenient enough to allow each breeder considerable leeway for his own standards. It remains an open question whether the average progress of the breed will be faster in the long run when each breeder is entirely free to work out his own ideas than when his standards of selection, even within rather broad limits, are partly forced on him by a majority of his fellow breeders working through selective registration administered by the breed association.

Selective registration requiring visual inspection of each animal would be costly in the United States because of the great distances over which most breeds are scattered. There would be some expense connected with maintaining the records of the inspections and administering the work, although the overhead costs of administration might be only a small addition to the regular costs of operating the secretary's office. There would probably need to be provision for appeal where the breeder was not satisfied with the inspection given his animals. From time to time ill feeling would arise when some breeder felt that the inspector was being deliberately unfair to him. It might be necessary to make provision for registering the offspring of rejected animals if those offspring were so meritorious as to prove the inspectors wrong.

Breeders of grade animals might be willing to pay increased prices for animals which were certified as to individual excellence as well as to purity of breeding. This might go far enough to cause some of the public to infer that all registered animals of the breed were of about the same merit. Anything which would cause the potential customer not to study the animals before he makes his selection, or which wonld tend to minimize attention to the breeder's reputation, has its possibilities of doing harm. It seems unlikely that selective registration would be carried far enough to make this danger important.

One commercial aspect of the situation is that some owners make more strenuous efforts than others to sell males to other breeders of purebreds. A certain amount of overhead in showing, advertising, and sales efforts is required to sell any large fraction of the males produced. In some cases those who make such efforts try hard to sell nearly all the males they produce, while others make little effort to sell males except to breeders of grades. The herds concerned usually do not differ that much in real breeding merit. The adoption of selective registration might restrict the efforts of those who are most active in selling males more than it would those who are not now active at that. Doubtless other unforeseen effects and complications will develop when selective registration is put into practice. Any association attempting it will need a trial period of several years to gain the experience necessary for making the plan operate successfully when applied to the whole breed.

From 1942 to 1944, the American Jersey Cattle Club admitted bulls to registry only if their paternal sisters or their dams had met certain production requirements or if the sire was a "star" bull. The sire becomes a star bull by his ancestors having met certain production requirements or if at least ten of his paternal sisters and his dam have been classified officially as to type and have scored high enough. There are four grades of starring, the four-star bulls having the most promising pedigrees, three-star bulls next, etc. In addition there are the unstarred bulls which have not enough production or type ratings among their near relatives to earn them even one star. Since 1944 the compulsory features involved in selective registration have been dropped but the starring plan is retained. Since 1944 the Ayrshire association lists progeny-tested sires in three classes of apparent merit but what the breeder does with this listing is optional with him.

SELECTIVE REGISTRATION IN OTHER COUNTRIES

Selective registration is practiced in many of the continental European countries. The rules for operating the plan vary but in general are somewhat as follows. The inspectors work under the direction of the farmers' co-operative societies or of the breed association. In either case there is usually some financial support from the government, accompanied by a small amount of governmental supervision to see that such money is spent in accordance with the laws appropriating it. The breed association maintains tentative registry books and permanent registry books. Soon after an animal is born it is entered in the tentative registry and at an appropriate time an inspector certifies to this animal's individual merit. It may then be placed in the permanent registry, or in some cases it may remain in the tentative registry as long as it lives and be placed in the permanent registry only after its death. Naturally the animals are not inspected until they are grown or at least well along toward maturity so that the inspector can be fairly certain of their mature individuality. Tentative registry is therefore necessary to keep the records straight. In the case of dairy cattle it is usually required that females shall produce a minimum quantity of milk or fat before they are finally placed in the permanent register and that males to be eligible for the register must be out of cows which have met production requirements higher than the minimum requirement which would entitle cows to entry. Sometimes the inspection by the committee takes place at the local fairs and sometimes the inspectors go from farm to farm systematically or upon request.

The countries where these selective registration systems are in operation are mostly countries where the breeds are native, and therefore the ancestry of the majority of the commercial stock differs only slightly from that of the pedigree stock. This makes more need for setting off, by some special requirement or inspections, those animals good enough to furnish future breeding stock than has been the case in the United States, where most of the pure breeds have been imported and at first differed greatly from the stock in the communities where they were introduced. In most of the countries where selective registration is in effect, the formal organization of the breed association occurred at a comparatively recent date. This contributes something to the feeling that there is no great gulf between the registered and the unregistered animals. Usually provision is made for admitting to registry high grades which are outstanding in their individual merit.

The following special items about selective registration in some other countries may suggest the special conditions encountered and the variety of ways adopted to meet them. They are by no means a complete account of the registration systems in use. The details of those are changed from time to time.[2]

GERMANY. German animal breeding practices and customs of registration were, of course, thrown into confusion by the war of 1914-18. The cow-testing associations and similar organizations were again operating on an extensive scale by 1924 or soon afterward. Since 1930 only cattle from herds which have been in cow-testing association work have been eligible to be shown at the national exposition. Since 1934 and especially since 1936 the compulsory features of cow testing have been greatly extended. In Hanover about 18 per cent of the cows were tested voluntarily in 1934, but under compulsory testing this rose to 83 per cent by the beginning of 1937. The German animal breeding law of 1936 brought about far-reaching control and compulsory inspection (Körung) of all classes of breeding stock. In many cases only one or two breeds could be kept in each district. This extended to sires used only in private herds, as well as to sires which were offered for public service. This system was not in operation long enough before the next war to demonstrate what effects it actually would have.

HOLLAND. The Netherlands Herdbook Association[3] at the Hague maintains four kinds of herdbooks: the calfbook, where service certificates and birth certificates are filed in order to keep the records of ancestry straight; the herdbook proper, to which animals are admitted on

[2] This is written in May, 1945.

[3] The Friesian Cattle Herdbook Association (with headquarters at Leeuwarden) has a slightly different procedure.

mature inspection; the advanced register for recording production; and the register of proved sires. The filing of service certificates soon after breeding is compulsory. The filing of the birth certificate must take place within a few weeks after the birth of the calf. Females are inspected and scored for entry into the herdbook proper soon after they drop their first calf. A score of 75 points out of a possible 100 is necessary for registration. Recording milk and fat production is not compulsory, but bulls are not accepted for registry unless they are from tested dams. Bulls are inspected and scored soon after they are 12 months old, before they go into service, but must be scored again after they are 24 months old. If a bull is accepted as a yearling but is rejected at the two-year-old scoring, the owner is allowed 30 days as a reasonable time in which to get another bull. All services made by the rejected bull more than thirty days after his rejection are treated as though the bull were a grade, but services made prior to that are accepted for purposes of registration. The inspection is so severe that about 55 per cent of all bulls offered for inspection are rejected. There is, of course, no way of judging how much selection the breeders have already practiced in deciding which bulls shall be offered for inspection.

SWITZERLAND. In Switzerland the physical conditions, especially the summer use of mountain pastures far from the home villages and the small size of many of the herds, compel more co-operation among breeders than is usual in the United States. Bulls must be shown at the large regional fairs for classification if the purchasers are to be eligible to receive the payments which the government provides for stimulating the use of improved sires. Such payments and other considerations are important enough that almost all bulls get shown at these large regional shows. Frequently as many as 1,300 Brown Swiss bulls are shown at one time at the largest fair. The cows are offered for inspection at the local or village fairs. Cows are scored during their first or second lactations, and those scores are printed along with their pedigrees in the printed herdbooks. The advanced registry records not only how much milk and fat the cow gave, but also how many hours she worked at draft purposes during the year. A considerable fraction of the Swiss cattle are used for milk, work, and beef, thus being in a sense triple-purpose cattle. Special stress is laid on longevity and regularity of breeding. Each cow which produces at least six living calves in the space of eight consecutive years is given a special distinguishing mark in the printed herdbook.

DENMARK. In Denmark there is widespread co-operation among farmers for many purposes, and the co-operative societies conduct the pedigree registration and other means of livestock improvement. Breed registry societies, such as those in the United States and Britain, do not exist. A committee of the union of co-operative societies directs the registration policies as the board of directors of a breed association would do in the United States. Of course, most members of this committee are breeders themselves or have in some other way made themselves thoroughly familiar with the practical problems which breeders encounter. Hence, the conduct of registration is not very different from that in the United States; but the committee members are responsible to the farmer co-operative societies, that is, to the customers who will use the improved breeding stock being produced. It has been agreed that 500 cows registered per year is a large enough number to supply the real needs of the breeders and farmers. The animal husbandry *consulents*[4] nominate something like twice that number of cows. Then the central committees consider the available data concerning these and discard those which seem least worthy until the number is reduced to 500. Cows rejected one year can be nominated again and perhaps accepted in a later year. No cow is considered until she has been in milk at least three consecutive years. No matter what her age when nominated, her actual uncorrected fat production must have averaged more than 400 pounds per year ever since she first freshened. The national committee in charge of swine breeding supervises the registration of swine. Registrations are accepted only for animals bred at the state-recognized swine breeding centers. Those are farms where the breeders have complied with certain regulations, including sending each year to the testing stations half as many test litters as they have sows in their herds.[5] At the testing stations these test litters (of four pigs each) are fed under standard conditions, and the rates and economy of gain are recorded. When each pig reaches 200 pounds, it is slaughtered at a nearby bacon factory and its dressing percentage and the type, conformation, and quality of its carcass are measured and scored. Also, each breeding center is inspected twice each year by a committee which scores it for: (1) management and general appearance of the farm, (2) conformation of the breeding animals, (3) fertility of the breeding animals, (4) efficiency in the use of feed by the test pigs from this center, and (5) slaughter quality of the test pigs from this center. The considerable costs of the swine improvement plans are mainly borne by the co-operative bacon factories. The plans are thus directed and financed indirectly by the customers who buy the improved breeding stock and not by the breeders who produce it. The government makes a small financial contribution

[4] Employees of the co-operative societies who provide technical advice on livestock matters, somewhat as county agricultural agents do in the United States, and also act to some extent as the business agents for their co-operatives.

[5] Lush, Jay L. 1936. Genetic aspects of the Danish system of progeny-testing swine. Iowa Agr. Exp. Sta., Res. Bul. 204.

to part of the work and extends legal authority where needed to the co-operative societies or to the co-operative bacon factories but does not itself take an active part in directing the work. Exhibiting at the fairs is not compulsory, but a large part of the breeders do that. The classification made at the fairs is entered in the herdbooks or other records pertaining to those animals, so that most pedigrees have in them considerable information about the type classification of the ancestors, especially of the sires. The central committees specify in detail the kind of records which each stockman, who aspires to be called a breeder, must keep. The committees or their representatives inspect those private herdbooks at certain intervals for accuracy and completeness. In some cases the owner is not permitted to make the entries himself but must keep the notes and papers concerning each event until the *consulent* comes on one of his regular visits, verifies them as well as he can, and makes the proper entries. This supervision and uniformity give the private herdbooks a semiofficial standing and make it unnecessary for the central committee to keep birth certificates or other records of that kind on animals not yet admitted to the national herdbooks.

These details will show something about how widely the pattern of selective registration may vary from country to country according to circumstances. If selective registration is adopted in the United States, still other devices will be needed to adapt it to the local needs and conditions.

AMERICAN APPROACHES TO SELECTIVE REGISTRATION

The Standardbred horse is an American breed which takes its name from the fact that in its early history animals must have been able to trot a mile in 2 minutes and 30 seconds or pace a mile in 2 minutes and 25 seconds before they could be registered. The Brahman Cattle Breeders Association (founded in 1924 and operating mostly in the coastal regions of Texas and Louisiana) requires inspection of animals before they are accepted for registry. The scores and other descriptive comments concerning each animal are filed with its registration in the secretary's office. No herdbook has yet been published. When the Jersey breeders established their Register of Merit in 1903, many of the cows were measured and scored as to type by some member of a group of about 19 authorized judges. These scores were not used, however, to determine eligibility for registry. They were intended to furnish evidence about the relation between type and production. Perhaps also some of the breeders then feared that unfortunate results would follow if the Register of Merit were allowed to operate with no attention at all to type.

Disqualifications. Many breeds have certain absolute disqualifications which are a bar to registry, even though the breeding is of undoubted purity. Thus, an Aberdeen-Angus which is red is not now eligible to registry; although red cows were eligible until about 1915. Red Aberdeen-Angus steers may still be registered to compete for prize money at the fairs. Neither is a red and white Holstein-Friesian nor one with black completely encircling the hoof-head eligible to registry. Most of these absolute disqualifications concern deviations from the peculiar type of that breed, which usually means details of conformation or color not directly affecting their usefulness as producers of meat, milk, eggs, wool, or power. No association will knowingly register an animal, either male or female, which is known to be a nonbreeder, except in the case of fat animals and geldings to be exhibited at shows. In none of the cattle breeds can a heifer born twin with a bull be registered until proof is furnished that she is fertile. This restriction is based upon the common experience that most such heifers ("free-martins") will be barren. Years ago some of the breeds had rules against registering offspring from dams which had formerly produced crossbred young to the service of grade sires or sires of other breeds. Only a few breeders actually professed a belief that this would affect the breeding value of subsequent purebred offspring ("telegony"), but the rule was placed in the by-laws of many associations on the long chance that there might be something to it. In 1924 it was removed from the by-laws of the last large association (a sheep one) which had had this rule. Breeders of dogs are reputed to believe more in telegony than breeders of other livestock.

Age Restrictions. Many American breed associations levy an extra charge on registrations not made until after the animal passes a certain minimum age. In some breeds the animals cannot be registered at all after they pass a certain age. One reason for this is to complete the registration before the breeder loses or forgets some of the facts in the case. The opportunity for fraud is also diminished by having the registration made promptly. More animals are registered than if registration could be postponed indefinitely without penalty. One unfortunate result is that some animals are registered young which would not be registered if the breeder could wait until he could see them as mature animals. A plan which promises to combine the advantages without the disadvantages of early registration is "deferred registration" such as that in effect with the Guernsey, Jersey, and Ayrshire breeds. Under this plan the breeder files a birth certificate soon after the calf is born. The fee for this is small. This birth certificate entitles the breeder to defer final registration until the animal is mature, without incurring any penalty for lateness.

VOLUNTARY PLANS. The voluntary Herd Classification plans of the dairy cattle registry associations in the United States embody some selective registration in the fact that the registration certificates must be surrendered on animals classified as poor and that bulls out of cows classified as fair are not eligible to registry. The Herd Classification plan also records the animals in several different classes of individual merit, so that one who does not know the animals may learn what the classification committee thought of their individuality. The type classification is printed, after the name and number of each classified animal, in the various printed herdbooks. This puts more meaning in pedigrees in which these classified animals appear.

A feature of selective registration in the Herd Improvement Registry of dairy cattle is that the breeder who surrenders the registration certificates for his poorest producers is entitled to have those omitted from the published average for the production of his herd. The extent to which this is actually being done may be seen from the fact that, in the first 13 volumes of the Holstein-Friesian *Herd Improvement Registry*, 14,733 certificates of registry were surrendered voluntarily. This was 10.3 per cent of the total number of cows on test. Of course, some of these surrendered certificates were for cows already dead or barren. Even so, the figures indicate some selective registration against the least productive animals even after the expense of registration has been met.

The Ayrshire Association registers bull calves under six months old for half price if the sire and dam, or the dam and paternal grandam, or all four grandparents are in the Ayrshire Advanced Registry.

Such individual registration of poultry as exists is mostly connected with records of performance in such a way that it is selective.

ABANDONED PLANS. In 1889-91 the Holstein-Friesian Association paid bounties of $5 each for the castration or vealing of bull calves which were eligible to registry. This was a systematic attempt to induce the breeders to discard their ordinary and inferior male calves. The plan was discontinued because nearly as many bull calves were registered while the plan was in effect as before, and it was a heavy drain on the association treasury, more than $20,000 being thus expended in the three years it was in effect.

The Hereford association in 1895 and 1896 had a rule that 10 per cent of all applications for registry of bulls from each herd should be rejected, but the Secretary had no guide as to which ones those should be. The ruling was repealed in 1897.

SUMMARY

Selective registration is a form of official mass selection which consists in preventing individuals deemed inferior from leaving any registered descendants. Such selection cannot do any more than the individual breeder *could;* it may do more than he *would* if left entirely to his own initiative. Collective wisdom, as imparted by the inspector, might help the less well informed and might be of considerable help to the customer. Probably it could not rise to the level of the ablest individual breeder's ability.

Selective registration is widely practiced in many foreign countries, but some of their conditions are distinctly different from those in the United States.

Some of the American associations are experimenting with devices embodying some voluntary principles of selective registration. Doubtless these will be carried farther if they are found satisfactory and if the problem of expense can be solved.

REFERENCES

American Jersey Cattle Club. 1941. Selective Registration.

Gardner, Malcolm H. 1932. Selective herd-book registration. Holstein-Friesian World, 29:411–12 and 428.

Van den Bosch, I. G. J. 1930. The scoring system in the Netherlands. Holstein-Friesian World, 27:337 et seq.

————. 1930. The Holstein industry in America. Holstein-Friesian World, 27: 283.

Wriedt, Christian. 1930. Heredity in livestock. (Especially pp. 151–67). New York: The Macmillan Company.