

depends his own work, which shows greater or less value of the animal. These factors are, however, not always perfectly known and a veterinarian examining the animal may have no knowledge of their true nature or value.

CHAPTER 17

Type and Production Records

Breeders pay attention to outward conformation in making their selections for two reasons. In the first place, they may want a certain type because it has a market value. If a market demand exists for a certain type, the breeder may care little whether that type really will furnish to his customers the maximum profit or other satisfaction. The fact that they want it and are willing to pay for it is the thing of immediate practical importance to him. In the second place, breeders may believe that type and productiveness are closely enough correlated that if one selects for type he will get at least part of the productiveness he wants.

In many cases, especially among meat animals ready for market, a certain conformation not merely indicates production but actually comes close to being production, since the desired production is largely a matter of sizes and proportions of various parts. At the other extreme are cases where the desired production depends far more on the quality and rates of physiological processes than it does on the sizes and shapes of organs or parts which can be judged on the live animal. The closeness of the correlation between type and production may be of any degree ranging from almost perfect in such a case as the width of the loin or thickness of the round on fat steers, through such relations as may possibly exist between width of head and width of body, to correlations which are practically zero. An example of a correlation which was once thought to be high but has since been found to be practically zero is the relation which a half century ago was widely supposed to exist between the escutcheon of a cow and her producing ability.

Reliance on type as a means of estimating productive ability may be necessary when reliable records of production are not available. Production records on most animals come slowly and expensively. Sometimes, as in poultry and dairy cattle, they are not available on both sexes. Even where production records can be fairly simple and complete, as in the case of cows and hens, it is still true that many purebred animals do not have their production recorded. The situation is still less satisfactory among meat and work animals, where productivity is not easily nor completely measured. A breeder often has an opportunity to buy an animal on which no production record has been made, or he

may have to sell some of his young stock before they are old enough to have production records. Such a breeder, even though he has more faith in production records as indicating an animal's productivity than in conformation as a similar index, none the less wants to make as much use as he can of the animal's conformation in estimating its probable productivity.

Type has some sale value in all classes of livestock. In extreme cases beauty may be the main object. This is often encountered in "pet and fancy stock," such as rabbits, dogs, pigeons, and guinea pigs, and is a prominent feature of some of the larger livestock such as saddle and coach horses. If the breeder's customers center their demand on type, he is of course interested mainly in that, and in productiveness only in that his animals should remain healthy and fertile. To appear healthy is, in most cases, an important part of the breed ideal for type also. If his customers are looking for productiveness regardless of beauty, the breeder is interested in type only as it may help him get that productiveness more surely and quickly than if he did not pay attention to type.

The stockman usually wants lifelong productiveness in each animal rather than a maximum single record from each, although the advertising value of an extremely high record may sometimes mean more financially to a breeder than a higher average record which does not become phenomenal in any one year. A single production record is not a perfect index of such life productivity, as was emphasized in chapter 13. The question of how much attention to pay to type and how much to pay to production records in selecting for lifetime productivity is, therefore, a question of comparing and combining two indicators, neither of which is perfectly accurate. Yet it would be a rare coincidence if the usefulness of the two happened to be exactly equal. The principles of estimating an unknown quantity from two known quantities which are partly correlated with it are such that a slightly more accurate estimate may usually be made by using both the known quantities than by using the more accurate of them alone, although the best proportion in which to weight the two is much affected by their relation to each other.

Each intermediate step weakens the effectiveness of selection. Thus, if we want to select for quality x , and it is correlated imperfectly with w , we will not come so close to getting x by selecting w as we would if we could select x directly.¹ If x cannot be observed directly but is rather

¹ As a numerical example, Rasmusson has shown (1930, *Nordisk Jordbruksforskning*, pp. 247-55) that even if the correlation between x and w is .8, one wishing to select a certain number of individuals which excel the population average in x by at least one standard deviation would need to examine 7.8 times as many if he selects them indirectly by looking for w as he would if he could select them directly by examining them for x .

closely correlated with y and not so closely with w , we would come nearer getting the value of x we want by selecting for y than by selecting for w . Unless w 's correlation with x is altogether due to w 's correlation with y , we would come still nearer to getting the desired value of x by selecting for both y and w ; but the proper amount of attention to be given to y or to w would depend upon how closely they were correlated with x and with each other. The guiding principle on this subject is that every needless intermediate step in selection should be avoided as far as possible but that a little is usually gained by paying some attention to other things besides the one which is most closely correlated with productivity. The very real danger in that is that one will pay so much attention to these minor things that he cannot pay enough attention to more important things which are more closely correlated with lifelong productivity.

THE CORRELATION BETWEEN TYPE AND PRODUCTION

In most actual studies of the correlation between type and production the correlation between one estimate of type or conformation and one production record of each individual in the population studied was measured. A few samples of those are mentioned in the following paragraphs.

When official testing began in the Jersey breed, certain judges inspected and scored the cows admitted to the Register of Merit. Gowen studied these data to see what correlation existed between the scores and the production records. Most of the correlations between the scores for each individual point of conformation and the actual production records of those cows were of about the magnitude of $-.07$ to $+.19$. The correlation between the production record and the total score of the cow ran somewhat higher, since it took into account all of the points scored. When the study was confined to the scores turned in by the nine judges (out of the nineteen recognized ones) whose scores most closely agreed with the milk yield of the cows, the correlation between their total score and the milk yield was $+.38$. While this is a real correlation, it was obtained only after discarding the scores of half of these men who were believed by the association to be competent to score the cows.

In similar studies on early Holstein-Friesian records Gowen used measurements made on some of the first officially tested cows. Table 14 presents the correlation coefficients he found between the seven-day milk yield and various body measurements and weights.

The maximum correlation between yield and any body measurement was $.36$. The correlations found were real and of some use in

selecting the high producers, but they were by no means as high as the correlations between different records made by the same cow. A considerable part of these correlations with measurements resulted from differences in general size. Within a breed the largest cows tend to be the heaviest producers and naturally tend also to have the largest measurements.

Engeler's study² of the yields of 455 Brown Swiss cows and their scores when they were inspected for registration showed a correlation of only +.04. In another study³ of 138 cows in one herd he found a correlation of +.32 between milk yield and score.

In dairy cattle there have been several studies of show-ring placings and production records, where both were known. Because only a small

TABLE 14
CORRELATION COEFFICIENTS BETWEEN SEVEN-DAY MILK YIELDS AND CERTAIN ASPECTS
OF CONFORMATION, AGE BEING CONSTANT (AFTER GOWEN)

Characters Correlated	Correlation Coefficient
365-day milk yields in different lactations.....	.66
7-day with 365-day milk yield (same lactation).....	.60
7-day with 365-day milk yield (different lactation).....	.46
Weight with 7-day milk yield.....	.42
Body length with 7-day milk yield.....	.36
Body girth with 7-day milk yield.....	.25
Body width with 7-day milk yield.....	.28
Hip height with 7-day milk yield.....	.24
Shoulder height with 7-day milk yield.....	.22
Rump length with 7-day milk yield.....	.18
Thurl width with 7-day milk yield.....	.01

range of types was included—no really poor types would be among those for which the placings were recorded—such studies throw little light on the correlation between type and production. They demonstrate that show animals can produce well, but so might many others if tested under the same circumstances.

A more suitable basis for studying the correlation between type and production is in such data as the Holstein-Friesian Herd Classification. Table 15 shows a summary of such data.⁴ The figures show that type and production do tend to go together in this population. On the average the fat production increased 24.6 pounds with each grade the cow was higher in the type classification. The correlation between the two

² 1933. Die Ergebnisse statistischer Auswertung 40-jähriger Herdebuch-Aufzeichnungen beim schweizerischen Braunvieh. Bern: Verbandsdruckerei A. G.

³ Schweizerische Landw. Monatshefte 19, No. 6, 1941.

⁴ As of October, 1942. The records are on a thrice-a-day mature basis and include the first 365 days of the lactation.

is a little less than + .2. That leaves plenty of opportunity for very high producers occasionally to be of poor type and for some animals of high type to be poor producers. The correlation in the general population of dairy cattle is probably a little higher than this, since, in the herds submitted for classification, most of the cows thought by their owners to be "Fair" or "Poor" in type already would have been culled

TABLE 15
AVERAGE HERD TEST RECORDS OF HOLSTEIN-FRIESIAN COWS AS CLASSIFIED FOR TYPE
UNDER THE HERD CLASSIFICATION PLAN

Type Classification	Number of Cows	Average Production	
		Milk	Fat
Excellent.....	261	17,215	601
Very good.....	1,377	15,988	554
Good plus.....	2,213	15,754	544
Good.....	2,138	14,960	514
Fair.....	426	14,316	488
Poor.....	25	12,612	431

unless their production was unusually good. On the other hand, part of the apparent correlation may have come about because large size gives an advantage, both in classification and in production. Also, the classification may have been influenced in some cases by knowledge which the classifying officer had of the cow's prior production.

Table 16 shows the summary of such data on Jersey cows to April, 1946 on a twice-a-day 305 day basis. The regression of fat production on type—the average increase in fat production with each increase of one grade in type classification—was 12.8 pounds which is only a little less than the 24.6 from the Holstein data when allowance is made for lactation length and times milked per day.

Engeler's conclusion from studies in Switzerland is: "Form, produc-

TABLE 16
AVERAGE HERD TEST RECORDS OF JERSEY COWS WHICH WERE ALSO
CLASSIFIED OFFICIALLY FOR TYPE

Type Classification	Number of Cows	Average Fat Production
Excellent.....	801	483
Very good.....	4,213	460
Good plus.....	6,060	448
Good.....	2,700	434
Fair.....	369	420

tion, and health are not so closely related that they can be substituted for each other as bases for selection. These three characteristics are to a high degree independent of each other and to a high degree are transmitted independently to the offspring. The goal of selection consists in preferring those animals which to the fullest extent possess all three characteristics, phenotypically as well as genotypically."

On poultry several studies have been made of the relation between body measurements and production or of the success which a man actually attains in attempting to cull out the poorest producers from each lot, dividing them into two groups and noting their production immediately after the culling. In the culling demonstrations the apparently high success is largely the result of immediately preceding conditions, whereby the man doing the culling is able to identify those which are laying at that time. Since the test pens are not kept for a full year afterward, he seems to have been remarkably successful in picking out the poor producers. It is somewhat the same situation as if one were to go to a dairy farm and rank the cows according to his estimate of their milk-producing ability. If his rankings were then compared with the cows' actual productions in the following week or two weeks, he would seem to have been remarkably successful; but much of this success would be due to the fact that he could tell which cows were dry and which were recently fresh at that particular time! The available evidence makes it seem doubtful that the relation between productiveness and conformation is really any closer in poultry than it is in dairy cattle.

Studies of the relation between weight, conformation, and pulling ability in draft horses have shown (Rhoad) correlations of about the magnitude of + .23 to + .35 between different measurements and ability to pull and + .45 between weight and ability to pull. However, nearly all of the correlation between measurements and ability to pull seemed to be an indirect result of general size, because the relation between these measurements and pulling ability within groups of horses which were all of the same weight was practically zero. In a similar study Brandt found that weight, age, and five measurements had a multiple correlation of .47 with maximum pull. Most of this seemed to depend on weight and height.

Studies of individual beef cattle have been less frequent because there is no one measure which comes as near expressing their real productivity as the actual production records of dairy cattle, poultry, and draft horses do in those cases. The studies which have been made show moderate or low correlations except for anatomical traits, such as fullness of round, which can be estimated closely when judged in the live animal before slaughter. There have been many studies of commercial

grades of groups of feeder steers as related to their subsequent performance in the feedlot. Usually the steers of the lower grades gain about as rapidly as those in the higher grades, but they sell at a lower price. Whether they are equally profitable to the feeder depends mostly on whether he can buy them at a low enough price. Because of the lower sale price, the lower commercial grades are less profitable to the man who breeds them.

Studies of type and production in sheep have been more numerous but have dealt mostly with the production of wool or with the feeding qualities of groups of lambs from the crossing of various breeds. Questions of type are often the subject of discussion among breeders of Merino and Rambouillet sheep⁵ and Angora goats.

Several experiment stations have conducted swine type tests which have shown differences in the rates of gain and in the kind of meat produced by swine of types varying from "very chuffy" to "extremely rangy." Studies of the ability of men to predict which pigs would make maximum gains have generally shown correlations of something around + .4 to + .7 between the estimate and the actual individual gain. These high correlations (compared with much lower ones on steers) are generally reduced to somewhere near the level of + .15 to + .30 when corrected for differences in initial weight. Greve⁶ studied eight different measurements on 205 sows of the Hoya breed near Hanover in Germany and concluded: "All the results show that it is not possible by using body measurement to find which sows have high breeding productivity."

Summarizing the actual evidence on the correlation between individual type and individual production, there is no complete analysis of the problem in any class of livestock; but the nearest approach to that has been in dairy cattle or poultry. In general, these studies have established the existence of correlations between type and production; but such correlations are generally much lower than the correlation between one production record and another production record of the same animal. The conclusion seems inevitable that if one is interested mainly in production he should pay much more attention to production records than to estimates of type, although it does not follow that he could afford to neglect type altogether. An actual production record is not quite a perfect indication of the lifelong production which is actually wanted. The emphasis placed by many men on outward evidences of health and "constitution" may have some justification in the relation of those to lifelong productivity. Many of the breeder's deci-

⁵ See Texas Bul. 657. Also Michigan Quart. Bul. 26:31-33.

⁶ Zeit. f. Zücht., Reihe B., 46:91, 1938.

sions must be made before he can know from actual experience what that animal's lifelong production will really be. Where type has any direct relation to lifelong productivity, the latter can be predicted more accurately by taking into account both type and production records than by using either alone, but the one which is least closely related to lifelong production should be given much less emphasis.

SUMMARY

A breeder may pay attention to type merely because it will add to the market value of the animals he expects to produce. Aesthetic considerations have much to do with the commercial value of some kinds of animals.

A breeder may also pay attention to type because he believes it to be a useful indicator of the lifelong productivity of the animal. Such indicators, even though not as reliable as production records, would be useful under a variety of circumstances actually encountered, especially among animals on which production records are lacking.

What is wanted is lifelong productivity. A single production record is not quite the same thing, although in most cases it is a more accurate indicator of lifelong productivity than is the individual's type, if either were to be considered alone.

Where type is related directly to productivity, a more accurate estimate of productivity can be made by taking type and the available production records both into account than by considering either alone, but there is danger of paying too much attention to the less accurate of the two indicators.

The practical problem confronting the breeder is to give the proper amount of attention to each. If he pays too much attention to type, the selection he can practice for production is automatically made less intense.

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CHAPTER 18

Breed Type

Breed type means the complex of external characteristics which is typical of a breed or is considered ideal for that breed. The term is often used in distinguishing one breed from another breed used for much the same purpose. Many ingredients of breed type are conspicuous details of conformation and color which have no relation to the economic productivity of the animals. Examples are the shape of horns in cattle, the dish of face and size and shape of ear in swine, color of face and shape of ear in sheep, and color generally. It is those features of breed type which are the subject of this chapter.

Attention is paid to breed type mainly because it is a "trademark" which is some additional evidence that the animal really conforms to the ideals of the breed. Probably the men who breed purebred animals average somewhat higher in honesty than men in most other lines of work, since the foundation of the pedigreed livestock business is the honesty of the men who sign their names to the pedigrees. Without general honesty on this point purebred animals could not command the premium they do. Yet there will always be a few mistakes and frauds. The existence of a definite breed type, especially if that is a combination of characters hard to obtain without absolutely pure breeding, is one check upon errors in registration. If a breed has a type of this kind, an animal deviating markedly from that type will be regarded with suspicion. From this point of view the breed type which is the hardest to attain or which is the most easily upset in crosses is the most highly prized. This often goes to extremes in the case of "fancy stock," such as pigeons, rabbits, or dogs, the desired type or standard being kept just high enough or changed just often enough that only a small proportion of the breed attain it.

Of course, breed type also is a matter of beauty to the men who have long been breeding and admiring that breed. But beauty is very much a subjective matter. Most of us can bring ourselves to think that any particular type is beautiful if we work with it and study it long enough and find it profitable. Naturally the breeders of other breeds may not

share our enthusiasm for the supposed beauty of our breed.

Part of the demand for breed type originates more or less unconsciously with breeders who are enthusiastically steeped in the tradition of the ancient purity of their breed. It is easy for such men to persuade themselves that "the best animals of the _____ breed with the purest blood are always thus and so," and to believe that deviations from that description indicate impurity of breeding or that something went wrong with the hereditary process.¹

Insistence upon conformity to breed type is actually harmful only as it weakens the intensity of selection for economically important points. This it must do to some extent.

An example of how insistence on breed type may change a breed is the occurrence of red spots on the faces and red rings around the eyes in the Hereford breed. Many of the Herefords imported to America carried these red markings. There was at first no prejudice against this; and, in fact, certain breeders rather preferred these, which they called "brown eyed." Eventually the tide of favor swung toward faces as white as possible. Today one sees few purebred Herefords which have complete red rings around the eyes. In the extreme southwest part of the United States, Herefords with pure white eyelids are more subject to cancer of the eyelid than are those with red eyelids. This is not an important matter, because only a small fraction of those with white eyelids develop cancer. Moreover, the cancer develops slowly and only upon the older animals. A ranchman usually has time to cull those affected and to ship them to market without suffering a complete loss. This is a minor disadvantage, but many ranchmen wish that the Hereford had kept its original high frequency of red-eyed cattle. Why did the Hereford breeders select the white-eyed type when there was no criticism of the utility of the red-eyed ones? The answer seems to be that among the very first things to appear in crosses of Herefords with other cattle were red spots on the face and red rings around the eyes. To many a cattleman, the presence of red spots on the face or red rings around the eyes of Hereford cattle indicated impurity of breeding. With this customer opinion confronting him, it was almost inevitable that the breeder of purebred Herefords should select for those which had the most nearly white faces and white eyelids.

Another striking case was the strong preference for yellow color in honeybees which arose soon after yellow Italian bees began to replace the black or German bees in the United States. Many beekeepers

¹ See W. Engeler's interesting account of the theory of "racial constancy" and selection for breed type in European animal breeding writings from 1800 to 1880. Pages 45-58 in "Neue Forschungen in Tierzucht," Bern, 1936.

inferred that the yellow color was itself *the cause* of the practical qualities—gentleness and superior honey-gathering ability—they wanted. They began to select for yellow color itself. Charles Dadant found in Italy some bees darker than most Italian stocks but more productive. These he could hardly sell to American beekeepers who had by that time come to believe that the yellower the bee the better. Who knows how many years the practical progress of beekeeping was retarded by that color craze!

Such examples are by no means confined to the United States. Even in Denmark, where such high emphasis is placed on practical utility in all livestock, the Red Danish cattle are not eligible for prizes at some of the important shows if they have a large amount of white or any roan color. The reason is that Shorthorn blood was used many years ago in some attempts to improve the Red Danish breed by crossing. In time that came to be regarded as a failure, and every effort was made to cull from the breed all animals carrying any traces of that Shorthorn out-cross. Who knows how much of the Shorthorn dislike for a dark muzzle in Britain and the United States today is a similar hangover from the controversy about the use of the "Galloway alloy" in the days of the Collings? Or how much of the Guernsey dislike (in the United States—little attention is paid to it in Guernsey) for a dark muzzle stems from a desire to emphasize the distinction between them and the Jerseys? Similarly, in Denmark the insistence of the breeders of Landrace swine that their swine shall have very large and drooping ears seems logically explainable only on the ground that this is one of the few outward distinctions between the Landrace and the more or less competitive Yorkshire, both breeds being bacon hogs, long-bodied, and solid white. In the tropical parts of Brazil, breeders selecting among pure zebu cattle try to get them with ears as long as possible. Presumably this is an aftermath of the extreme competition which prevailed when the zebu cattle and their grades were first getting a foothold. The grades with the most zebu blood generally had the longest ears. Hence length of ear, originally preferred because it indicated a high percentage of zebu blood, came finally to be considered as itself a sign of higher merit.

Some of the things which constitute breed type cannot be fixed. Laboratory experiments with various piebald races of animals such as guinea pigs, have shown that a considerable amount of variation in extent of white spotting is not hereditary at all and would still exist in a homozygous strain or pure line. There is every reason to think that the same situation prevails in such spotted breeds as the Holstein-Friesian or Guernsey or Spotted Poland-China. No amount of selection, no matter how long continued or with what inbreeding system it was com-

bined, could ever produce an absolutely uniform breed. This is in spite of the fact that in these breeds there are modifying genes which tend to restrict or extend the pigmented areas. Doubtless the same thing is true with spotting which takes a more definite form as, for example, the amount of white in the Hereford pattern or the amount and uniformity of the white belt on Hampshire swine.² Wherever this is the situation and the breed type is really unfixable, it is especially regrettable when otherwise desirable animals are discarded from the breeding herd on account of failing to conform closely to a rigid standard of color markings. Not only are their good qualities lost to the breed but, ironically enough, their discarding does not cause the breed to conform more closely to the standard breed type than if they had been kept for breeding purposes.

The matter of breed type is receiving less attention from breeders today than it has many times in the past. The practical breeder cannot afford to neglect it altogether wherever it still has some cash value in the market in which he must dispose of his surplus. He needs to satisfy his customers as much as he can without losing much real productivity from his stock. Any more efforts in selecting for breed type than his customers' demands absolutely force on him detract from his ability to select for things of practical utility. When a breeder hears that his customers very much want certain features of breed type, it behooves him to be skeptical about whether they really will pay him much more for the animals which have those things. Some statements of this kind are just sales talk or buyer's talk³; others are details in an almost endless and unbalanced catalogue of all characteristics which ever have been noticed. Many of these details will have little or no detectable effect upon the amount the buyer really will pay.

SUMMARY

Breed type serves as a trademark, which is to some extent additional evidence of purity of breeding over and above the printed pedigree. It is not as valid evidence on this point as is sometimes believed.

Some of the elements of breed type probably cannot be "fixed" so that they will be perfectly uniform. Effort spent in breeding for those not only weakens selection for more important things but even fails to improve breed type.

Breed type becomes positively harmful when so much attention is paid to it that animals above the average in real usefulness are dis-

² For a plausible genetic explanation of white belt in swine, see Olbrycht's article in *Annals of Eugenics* 11:80-88, 1941.

³ *Proverbs* 20:14.

carded because they do not conform to breed type in matters which are of little or no economic importance. The more points considered in selection, the less effective can selection be for each of them. Breed type should be kept in a minor place, but the practical breeder cannot afford to ignore it altogether if his market places some value on it.

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CHAPTER 19

The Show Ring and Animal Breeding

The original purpose of fairs was to provide a place for trading. In some parts of Europe, even yet, the man who has a few animals for sale may take them to a weekly fair. If no buyer makes an acceptable bid, he takes them home again to wait for the next fair. It is a small step from exposing animals for sale to exposing them for having their merits appraised by other breeders. The exhibition of animals not intended for sale was a prominent part of animal breeding practices even as far back as the early history of the Shorthorn breed. Charles Colling's famous "Durham Ox" was started in 1801 on a tour of exhibition which lasted for six years. This tour was more like the sideshows than like the show rings of today. The Colling-bred "White Heifer That Trayeled" started on a similar tour a little later. The Booths were famous for showing their breeding stock at many fairs. Thomas Bates on occasion exhibited his Shorthorns and prided himself on his ability to judge, although he was outspoken in his criticisms of the evils of overfitting and of keeping cattle just for showing. According to Wriedt, the first public show corresponding to our modern livestock shows was held in 1798 in Sussex, England. The first public show in Denmark for all kinds of livestock was held in 1810. The first public show in Wurtemberg was in 1817. Most of this early showing was for advertising purposes, and the premiums offered were small or consisted only of trophies. According to Jull the first poultry show in the United States was held in Boston in 1849. Poultry showing in England began at about the same time.

THE SHOW RING IN RELATION TO BREED IMPROVEMENT

There are two ways in which the show ring may affect breed improvement. First, it may keep the breeders informed about the ideals of the breed. If they use that information in their own selections, the show ring can be an important factor in guiding the direction in which the breed is to be changed. Secondly, the show ring might be used to find the best animals in the breed to such an extent that breeders could accept the show ring placings as guides in buying and selling their

breeding animals. While this condition, of course, is never entirely reached in any land, yet the advertising and popularity which certain animals may acquire through their high winnings in the show ring may go far to get them or their sons or daughters used extensively in many herds which otherwise would never have sought them. This may have some effect upon the genetic composition of the breed if it is done year after year, since it constitutes a mild grading-up process toward the prize winners and the herds from which they came. This is a form of selection favoring the genes which are most frequent in the type of animals which the judges place highest. Even though the judge sees but a tiny fraction of the animals of the breed, his approval or disapproval may help determine which animals become paternal grandsires or great grandsires of the breed. Since one herd rarely is a prominent prize winner for more than a few years, this does not often emphasize any one animal or family in a way which could be called linebreeding. It is emphasis of an ideal, rather than emphasis of an animal.

In the shows in the United States and Britain, the main object is to emphasize the visible ideal which is held by the breeders of each breed. No attempt is made in American and British shows to judge pedigrees. The few attempts to give some weight to production records, in addition to what is visible to the judge, have met with only partial approval from those who tried the experiment. The shows, especially the larger ones, give tremendous emphasis and advertising value to championships and first places, out of all proportion to the usually small differences in real merit between first and second or third place animals. The main thing is to exalt before the public the most nearly ideal combination of visible characteristics which can be found and to give the breeders a clearer picture of the perfect animal to guide them in their own selections. It is only incidentally that attention is directed to the animal for its own sake. The major fairs in the United States usually perform well this function of exalting the ideal. The larger fairs do not give much help to the beginning breeder, since the placings he sees mostly concern small differences between animals nearly all of which are good ones, and the interest in judging is mostly centered on the placings of the top two or three animals.

In the 4-H Club shows in the United States and in many of the shows in continental European countries, there have been earnest attempts to remedy this and to make the shows a place of instruction in judging from top to bottom. This is intended to benefit the large part of the public and the considerable fraction of breeders who have not become experts in judging and perhaps never will, but who wish some information or training in the kind of judging they themselves can do

in their own herds. In their applications of judging they may have an opportunity to cull perhaps the poorest third or fourth of their females; or perhaps they must select a sire from among a group of moderately good males, no one of which is really of championship caliber. The devices used to make these shows more instructive to the beginner and to the general public mostly concern: placing all animals shown, no matter how poor they are; having grades or descriptive terms which are kept as nearly constant as possible from show to show and from year to year so that the written record of the animal's show ring placings may have a standard meaning; stabling or tying the animals during the fair in the classes and in the order in which they were placed so that visitors may see and study the placing at any time during the fair; minimizing showmanship in the placings; and having as many breeders participate in the judging as is reasonably possible. It is probable that some of these practices can with advantage be adapted to American conditions for those shows where a majority of the animals come from nearby farms and where most of those who show are relatively inexperienced.

The show ring can do only a small amount toward ranking the animals of the breed in the order of their real breeding value. In the first place, only a tiny portion of the total number of animals of the breed are shown. Table 17 shows this in a general way, using Iowa as an example because its state fair is large and there are many purebred animals in Iowa. The figures in this table give only a rough idea of the extent of actual participation in showing, however. Besides the qualifications listed under the table and the fact that the years are not identical, many of the exhibitors and animals were from outside the state.¹ In the second place, differences in showmanship, grooming, and such things may affect the animal's show ring ranking, although they have no bearing on its breeding worth. Such practices may even prevent the judge from ranking the animals as nearly in the order of their breeding merit as he could if no preparation for showing were made. An example is length of wool, which is an important part of the practical merit of a sheep, especially of sheep of the Merino and Rambouillet breeds. Yet the length of fleece which the sheep wears when it enters the show ring may be so altered by shearing early, stubble-shearing, blocking and trimming, etc., that the judge cannot afford to pay as much attention to it in the show ring as he usually would if he were culling his own sheep where he knew that all had had substantially the same length of time in which to grow the fleeces he saw before him. In the third place, the

¹ In Denmark, where participation in the fairs is more general and each owner can show only in the district where he lives, about 6,000 bulls and 10,000 heifers and cows altogether are shown annually. This is about 7 or 8 per cent of the bulls but only about 0.4 per cent of the females among all the cattle of Denmark over one year old.

temporary condition of the animal must count for much because of the judge's duty to set before the public an animal which at that very moment comes nearer the visible ideal of the breed than any other animal in the ring. In the fourth place, the judge's ability to find the best breeding animals, even if these other obstacles could be overcome, is limited, of course, to the correlation which exists between outward appearance and real breeding value. In the fifth place, it is difficult to compare a placing in one show with a placing in another unless one was present at both shows and remembers what kind of animals were present at each. What comparison could one make from the information

TABLE 17
NUMBERS OF REGISTERED ANIMALS IN IOWA IN THE 1930 CENSUS AND NUMBERS
EXHIBITED AT VARIOUS IOWA FAIRS FROM 1930 TO 1936

Kind of Animal	Farms or Breeders Concerned		Number of Animals		
	Farms With Registered Females in 1930	Exhibitors* at State Fair in 1936	Registered Females on Farms in 1930	Registered Animals Exhibited at State Fair in 1936	Average Number Exhibited at County and District Fairs Each Year, 1930 to 1935†
Draft horses.....	1,974	72	5,241	383	4,355‡
Beef cattle.....	5,556	113	60,685	713	12,809§
Dairy cattle.....	5,297	112	33,272	719	
Dual-purpose cattle.....	437	19	4,003	200	4,551
Sheep.....	1,352	73	15,677	830	
Swine.....	7,446	226	66,189	2,238	15,118

* Including 4-H Club members who exhibited registered animals.

† The number of these fairs ranged from 76 to 82, averaging 78 in the six years. The number exhibited each year is the sum of the numbers exhibited at each of these fairs. Each fair was about two to four days in length, and they were scattered over a period of about nine weeks during August and September. Doubtless many animals were exhibited at more than one of these fairs and hence are counted more than once in these numbers, but no way was found to estimate how many of these duplications there were.

‡ Includes all horses without distinction between light and draft horses.

§ Includes all cattle.

|| All registered animals, whether male or female.

that one sire won first as an aged bull at the Page County Fair in 1935, a second sire was third as a two-year-old at the Iowa State Fair in 1933, while a third sire stood tenth as a Junior Yearling at the National Dairy Show in 1931?

Probably the ideals of the show ring are usually those of a majority of the breeders, but it is not certain whether that is because the show

ring leads the breeders or whether it merely reflects their current opinions after those have been formed by other circumstances, just as the driftwood on a river shows the course and speed with which the water moves but does not cause or guide that movement. Changes in ideals do sometimes occur; sometimes those get well started even against the disapproval of the current show ring ideals. A case of that was the marked change in ideals in the Poland-China and most other American breeds of swine between 1910 and 1920. When such changes are in process, the show ring may help them to spread more rapidly by giving the breeders occasion to meet and discuss the subject with examples before them.

In spite of its imperfections, no good substitute has yet been devised for the show ring as a means of indicating what kinds of individuals are best in the breeds of beef cattle, hogs, sheep, and draft horses. Even in animals such as dairy cattle and poultry, where there are reasonably simple and accurate tests for production, the show ring has not been displaced by these tests. Among all farm livestock, the Thoroughbred and Standardbred horses come nearest to relying upon production records with little use for shows. Among poultry breeders there is a rather wide gap between those who breed for production and those who breed for show. In dairy cattle there is a similar but less extreme divergence of opinion as to the usefulness of the show ring.

SPECIAL FEATURES OF SHOWS IN CONTINENTAL EUROPEAN COUNTRIES

Brief mention will be made here of some show ring practices in non-English-speaking countries. Some of these might be useful, especially in local fairs, if adapted to American conditions, or may be interesting because of their distinct contrast with the practices common here.

All animals exhibited in a class are usually placed from top to bottom, although it is permissible for the judges to indicate that two or more are equal. The animals are usually divided into at least three and not more than five classes. Prize money and usually the permanent records make no distinction between animals in the same class. Thus, in a single class of bulls there may be four "first prize" bulls, six "second prize" bulls, five "third prize" bulls, six "fourth prize" bulls, and three judged too poor to receive any prize. Those who are at the fair will know the individual ratings within each class. Those individual ratings are printed in the list of awards prepared immediately after the judging is completed; but they may not go into the permanent records and will not appear in the pedigrees of descendants of these animals. In those pedigrees it will be stated simply that this animal was "second prize" at a certain fair in a certain year. Every reasonable attempt is

made to keep the standards of judging constant so that "second prize" will mean the same thing at all fairs in all years in any one country.

In the case of cattle and horses, classes which are judged together are tied together during the daytime in the order of their placing until the fair is over, so that a visitor can study at almost any time during the show the placing in any class in which he is interested. He does not need to be on hand to see it judged. Physical difficulties may prevent that with swine and sheep. Over each animal or pen is posted prominently its classification and often its score, perhaps accompanied by the judges' criticisms and commendations of certain things about it. The catalogues contain for each animal the production records and scores or classifications of its ancestors.

Sometimes pedigrees are classified or scored also. Practice varies about whether (1) the pedigree score and the individuality score are combined into a single net score for the animal, (2) separate prizes are given for pedigree classification and for individuality classification, or (3) the prizes are given only for individuality, while the pedigree scores are printed merely for information. Since 1930 at the German national show cows must have records of production to be eligible for showing.

Many breeders participate in the judging. Sometimes they work singly and sometimes in committees. Where the classes are large, there may be almost a separate committee for every class.

Much use is made of progeny groups of one kind or another. Those vary more in the rules as to numbers required, etc., than do the "get-of-sire" and "produce-of-dam" classes in American shows. At some of the Danish shows at least two-thirds of the progeny of an older bull must be exhibited if he is to gain a prize for type. Some of those progeny groups may be judged on farms before the show. That is often done with stallions.

Showmanship is minimized in many ways. Usually the attendant makes little effort to pose his animal. In the bull shows in Switzerland the judging is done behind closed gates and not even the owner is allowed to be present. When the judges finally get a class placed in what they believe is the correct order, the bulls are allowed to stand for a while tied to the rail. Then the judges come back to look for defects which may become evident after the animals have stood for a time, and to make sure that the placing is satisfactory. The judging takes place in the first half day in these Swiss shows, but the animals must remain on exhibition during the daytime for three or four days.

In many countries there is more selling of exhibited animals than is usual in the United States. More than half of the bulls at these Swiss shows may change owners before the show is ended. In the Argentine

shows nearly all prize-winning animals are auctioned afterward. The owner may withhold his animal from the sale if he wishes, but this is not often done. In case he does that, the owner pays the management a fee to cover expenses and to pay the auctioneer what he would have received if this animal had been sold.

BUSINESS ASPECTS OF THE SHOW RING

The show ring is one of the best channels for advertising surplus stock. Many potential customers will not inquire whether the animals which won the prizes are closely related to those which the breeder is offering to sell them. Because of this, breeders who have many animals for sale can sometimes pay large prices for good show animals owned by some one who is not intending to exhibit them. The money thus spent is an advertising expense, just as surely as if it had been spent for newspaper space. It may be profitable if it helps keep the name of the breeder before his potential customers in a favorable light and if he has many animals to sell.

The show is an excellent place to meet other breeders and exchange ideas and experiences which may be of considerable practical value. In this way one can do much to keep informed on matters of concern to the breed and can learn of events or changes of reputation which he would not otherwise learn so soon. Sometimes the members of the breed association present will hold a meeting some evening after the judging is over to discuss matters which can be handled only in a co-operative manner.

The show ring provides an opportunity to learn judging, at least among the better animals, or to keep up to date the judging knowledge one already has. One will learn much by standing at the ringside, making his placing before the judge does, and then trying to see why the judge's placing was different from his own.

The practice of fitting out a show herd and going from one show to another on a long circuit insures that the average show ring merit of the individuals exhibited at each fair shall be higher than if there were no circuit system. Thus the show ring will more nearly achieve its object of showing the public the ideal which is held by each breed. Against this must be balanced the fact that it tends to destroy local participation in the fair. Many a breeder, who might take his animals to the nearest fair if he did not have to compete with professional showmen, will leave his animals at home and go to the fair as a ringside spectator under the present system. The long circuits promote professionalism in showing because the skill of the showman has a chance to be rewarded in many shows, not merely in one. The high rewards for success in professional

showmanship are an incentive toward such practices as surgical operations to correct defects and toward all manner of deception in showing the animal. The show tends to become more of a contest between showmen and less of a court of inquiry as to which animal really would be most useful for further improving the breed. In doing so, it may acquire some of the sporting interest which attaches to a horse race, but it becomes less useful to agriculture. The long show circuit may keep the herd away from home for a long time when the animals should be used for breeding.

Professional showmen sometimes take advantage of the circuit system by exhibiting several different breeds of the same species of livestock, especially at fairs where the competition will be light. This is particularly common with exhibitors of sheep where prize money is offered for so many different breeds. Such show herds or flocks are sometimes called "carnival outfits" or "gypsy herds." Few men are successful breeders of more than one breed of each kind of livestock. The most which can be said in economic justification of the carnival outfit is that it will advertise a breed in a region where that breed is little known. This may lead to some increase in sales by breeders of that breed and at rare intervals may be the means of introducing to a region a breed which has some real usefulness there but would not otherwise find a foothold so soon. The managers and directors of fairs are usually reluctant to reduce the prize money offered for the rare breeds to quite as low a level as would be proportional to the number of them which are bred in that region.

Many animals which played a prominent part in breed history were themselves prize winners, but there have also been some which were not shown or did not place high and yet did have more influence on the breed than any of their contemporary prize winners. Champion of England, who, more than any other one animal, was responsible for the "Scotch type" of Shorthorn, was of doubtful individual merit as a calf and was nearly discarded without being tried as a sire. In the Hereford breed Anxiety 4th was not shown, although it is said that he was an excellent individual. His owners regarded him as too valuable to risk fitting for showing. His sire, Anxiety, had been lost in just that way. Many of the sons and grandsons of Anxiety 4th were shown, but Beau Brummel, the grandson who became the most influential animal of the whole breed, was shown only once and placed fifth in his class that time. It is related that he would have ranked higher if he had been especially fitted for showing. The noted Shorthorn sire, Avondale, was fourth in his class at the 1908 International but later, as a sire, excelled the three which placed above him. It does not seem that any valid general conclusion can be drawn from such individual cases. They demonstrate

that show ring ranking is not an infallible guide to future success as a breeding animal, but not even the most enthusiastic admirer of the show ring would maintain that it is.

Whether an animal has an important influence on a breed depends on the opportunity it has and on chance circumstances, as well as on the kind of heredity it really has. As a rule those animals which stand high in the show ring are given a better opportunity as breeding animals than those which do not stand so high, but there is much variation in this. The financial circumstances of their owners and other incidental circumstances, which have no relation to an animal's breeding worth, are often the controlling factors in determining what influence an animal shall have on the breed. The Hereford bull, Beau Brummel, and the Aberdeen-Angus bulls, Black Woodlawn and Earl Marshall, were offered for sale to grade herds while yet young; but, fortunately for their breeds, the sales were not completed and the bulls were used for many years in purebred herds. The Percheron stallion, Brilliant 1899, was used for nearly a dozen years in France and then was sold to America, where he was used but one year on purebred mares.² After that he was used for nearly 15 years on grade mares only. The colts he sired in France and the kind of grade colts he sired in the latter half of his life indicate that the history of the Percheron breed might have been materially different if he had stood at the head of a stud of purebred mares during the latter half of his life. It is said³ that Mr. Gentry once offered to take \$25 for Longfellow, the Berkshire boar who afterward became the most famous sire of his breed. In fact, the buyer, who was merely looking for a boar to ship to a tenant, was given his choice of two pigs at that price. Mr. Gentry, trying to help him out, suggested Longfellow and the suspicious buyer promptly chose the other pig!

Since differences in visible merit are partly determined by the genes the animals have, it is to be expected that, if all animals were given equal opportunity, prize winners would usually have a higher proportion of prize-winning offspring than would breeding animals which were not prize winners themselves. But the animals' opportunities to be shown and to be used for breeding are different and little is known definitely about the heritability of differences in show ring merit. Rice found .21 for the regression of daughter on dam in the official type classification of Holstein-Friesians but herd differences in environment might have been responsible for more of this than heritability was. Proportion, symmetry, and balance are emphasized so much in the

² See pp. 237-39 in *A History of the Percheron Horse*, by A. H. Sanders and Wayne Dinsmore, Chicago, 1917.

³ Page 6 of *The Breeders Gazette* for February, 1932.

show ring that epistatic gene interactions seem likely to be important causes of differences in show ring placings. For these reasons it is impossible to say how many more of the offspring of prize winners will be capable of winning prizes themselves than will be the case among the offspring of those which did not win prizes. There have been many studies of the pedigrees of groups of prize winners, but only a few of these have included comparisons with the pedigrees of a representative sample of the whole breed. Those few have indicated that the pedigrees of the prize winners are substantially the same as the average pedigrees of the breed, so far as concerns ancestors much more than two or three generations back in the pedigrees.⁴ Some of the animals prominent as parents, grandparents, or great grandparents of the prize winners have not been so prominent in the average pedigrees. It seems possible to interpret this either as meaning that the prize winners come largely from only a few contemporary families to which the breed will later be graded up, or as resulting incidentally from the fact that only a few owners make a regular practice of showing at the large fairs, and any sires used extensively in their herds will almost inevitably be prominent in show ring winnings a few years later. In either event, it can hardly be maintained that the prize winners constitute very distinct families or strains within the breed.

SUMMARY

The show ring is a means of emphasizing the current ideals of the breed. If breeders are guided much in making their own selections by noting the types of animals which are placed high in the show ring, the show ring can have an important part in guiding the direction in which the breed average shall move.

It is not certain whether the show ring really causes the changes in the ideals of the breed or merely reflects the ideals currently held by a large portion of the breeders. There have been times when the breed ideal changed, even against opposition from the show ring. Probably the show ring cannot lead the whole breed far in a direction contrary to the ideals of the commercial breeder.

To a limited extent the show ring may help in rating the animals of the breed according to their breeding value. It is not very effective in this because: (1) the correlation between outward appearance and real productiveness is low for many characteristics; (2) so few of all purebred animals are shown; (3) considerable attention is paid to fitting, to temporary conditions, and to showmanship; and (4) many important things about which the breeder may know, such as amount of milk and

⁴ *Jour. of Heredity*, 22:245-49, and 27:61-72.

fat produced by dairy cattle, number of pigs weaned by sows, length of fleece on sheep, etc., must for practical reasons be given only a little attention by the judge since he cannot know exactly what those were.

In spite of these limitations there is not yet any good substitute for the show ring in measuring the general merit of the meat animals. Even breeders of animals which, like dairy cattle, have reasonably complete measures of productiveness not connected with the show ring continue to make extensive use of shows.

In a business way the show ring is an important means of advertising. The fairs offer opportunities to make sales and to exchange news and ideas with other breeders.

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CHAPTER 20
Likeness Between Relatives—Degrees of Relationship

The idea of relationship is familiar to all. Proverbs such as "Like father like son," "A chip off the old block," "What's bred in the blood will out in the bone," and "Blood will tell" are found in every language. Their antiquity attests the fact that people have always known in a general way that offspring tend to resemble their parents, and that brothers and sisters show many of the same "family characteristics," and that more distant relatives are usually less like each other than close relatives are. Genetics itself is defined as "the science which seeks to account for the resemblances and differences exhibited among organisms related by descent."

The first scientific attempts to measure the degrees of resemblance between different kinds of relatives were made late in the last century by Sir Francis Galton and his associates. In fact, correlation coefficients and many of the modern statistical methods now used for other purposes, too, were devised by them primarily for this purpose. With the rediscovery of Mendelism, interest in heredity shifted from the biometrical method to studies of the transmission of individual genes and, for a time, it was even supposed that the two points of view were antagonistic. Within recent years many of the statistical consequences of the Mendelian nature of inheritance have been explored, and the two fields of knowledge have been unified, each complementing the other.

THE BASIS OF RELATIONSHIP

Relatives resemble each other in various degrees because each offspring gets a sample half of the genes which its parent had. Relationship between two individuals is simply probability that, because they are related by descent, they will be alike in more of their genes than unrelated members of the same population would be. Closer relationship merely means higher probability of genetic likeness.

The parent-offspring relationship is the simplest one. It is fundamental in the sense that all other relationships are combinations of chains of parent-offspring relationships. In populations where there is no inbreeding, the parent-offspring relationship is 50 per cent, simply

because each offspring has received half of its genes from each parent.¹

Half of the genes of each offspring are identical with half of the genes of each parent, since the offspring received them from that parent. The rest of their genes (those which the parent did not transmit to this offspring and those which the offspring received from the other parent) may or may not be alike, just as two individuals of the same population may have some of the same genes merely because those genes are common in that population. Where there is some inbreeding these other genes will have some extra probability of being alike also. The extra relationship which inbreeding may cause will be discussed in the next chapter.

Half brothers are 25 per cent related because, on the average, one-fourth of their genes are duplicates which both received from the common parent, another fourth also came from that parent but are opposite members of the pair it had, while the remaining half came to each of them from the parent the other one did not have. This half of the genes are no more and no less apt to be alike than if the half brothers were unrelated members of the same population.

The most probable situation among a pair of full brothers is that one quarter of their genes will be duplicates received from the sire, another one quarter will be duplicates received from their dam, another quarter will have come to both from their sire but in each locus the genes will be opposite members of the pair he had, while the other fourth will have come to both from their dam but will be opposite members of the pairs she had.

This fact that pedigree and heredity are not identical was known before Mendelism but was then regarded as a mystery. Now we know that it is a natural—indeed an inevitable—consequence of the segregation of genes in parents which are not completely homozygous. However, anachronistic traces of the older view still persist in our speech and writings. Wonder is still sometimes expressed when two brothers are noticeably unlike, or such unlikeness is inferred to be evidence that the characteristic in question is not hereditary. In our everyday speech and among persons unfamiliar with genetics it is not yet generally appreciated that even for a perfectly hereditary trait (one unaffected by environment, dominance, or epistasis), full brothers or parent and offspring will usually differ in half as many of their genes as will unrelated members of the same population.

The probabilities stated for half and full brothers are averages; that is, they are more likely to happen than any other one result. Yet the

¹ Modifications of this for sex-linked genes will be discussed later in a separate section.

laws of chance cause some pairs of paternal brothers to receive more than one quarter of their genes as duplicates from their sire, while other pairs of brothers get less than one quarter. Although the average or most probable result remains at one quarter, it is theoretically possible for paternal brothers to have received anywhere from none to 50 per cent of their genes as duplicates from their sire. But if the number of genes is large, either of these extreme happenings would be very rare. The standard deviation of individual cases around the expected average of 25 per cent is $25/\sqrt{n}$ per cent where n is the number of independent pairs of genes involved. With $n = 25$, for example, about two-thirds of all pairs of paternal brothers would have received at least 20 and not more than 30 per cent of their genes as duplicates from their sire.² That still leaves room for some individuals actually to be noticeably more alike in their genes than others which have the same expected relationship. If we are interested in only one or a very few pairs of genes, such as the pair for the black-red contrast or the pair for the horned-polled contrast in cattle, relationship will mean little for a single pair of animals. However, even for a single pair of genes, the relationship figure will become dependable if we want to describe the average situation in a large group of pairs thus related.

Each additional generation, which intervenes in the line of descent through which two individuals are related, halves the fraction of their genes which are likely to be exact duplicates received from the ancestor which they have in common. That is why any one line of relationship between two animals gives an amount of relationship which is $1/2$ raised to the n th power, where n is the number of generations (Mendelian segregations) intervening between the two animals in that line or path of relationship. If they are related through more than one line of descent, each such bit of relationship must be evaluated separately. Then these are added to obtain the total relationship.

Two individuals chosen at random from the population which is used as the basis for computing the relationship would have many genes alike, merely because those genes are widespread in that population. Among pairs of allelic genes chosen at random, q^2 will be AA and $(1 - q)^2$ will be aa , leaving only $2q(1 - q)$ of such pairs to be unlike. Relationship between two individuals is the *extra* likeness due to common ancestry. It shows what fraction of those genes which would be

² Linkage makes the n of this formula something more than the number of different linkage groups but less than the total number of genes involved. With 20 to 30 pairs of chromosomes in most farm animals, an effective n of something like 25 to 100 appears reasonable for considering the reliability of individual relationship coefficients when the animals' whole genotypes or their heredity for complicated characteristics are being considered.

unlike in pairs of individuals chosen at random from this same population are probably alike in the related pair. The average genetic likeness between random animals of this population is the zero point on the scale on which relationship is measured. Zero relationship does not mean absolute unlikeness in every gene any more than zero on the thermometer needs to mean the coldest temperature possible, or sea level means the lowest altitude possible.

The question of what population should be used as the base or zero point for measuring relationship in any particular case thus has some importance. In considering evolutionary questions, the population might logically be the whole species or even a larger group of some extremely remote date. This is what the taxonomist means when he says, for example, that sheep are more closely related to goats than they are to cattle but are more closely related to cattle than they are to horses. But in applying the idea of relationship to individual animals or herds, we never carry it back to such a remote base, partly because pedigrees necessary for computing relationship are not known that far back, partly because chance variations from the most probable distribution of genes will in some cases have been in the same direction in successive generations and can have become large, and also because the time involved in evolutionary questions is so enormous that selection and even mutation have had opportunity to produce important changes which would not show in the pedigrees. The most remote bases we actually use in animal husbandry are in connection with the history of different breeds where we may, for example, group the Jersey and Guernsey together as "Channel Island breeds," or group together the black and white lowland cattle of the regions along the shores of the North and Baltic seas as a group of breeds more closely related to each other than they are to the Channel Island breeds or to the mountain breeds of central Europe.

The most convenient population to use for a base in animal breeding problems with known individual pedigrees is usually the breed at a date not often more than four to six generations in the past. For example, two Shorthorns might be "unrelated" relative to the Shorthorn breed in 1910. This is the same thing as saying that they are probably no more and no less alike genetically than the average pair of Shorthorns chosen at random from among those born in 1910. Yet, if their pedigrees were traced further, they might be found to be related 20 per cent relative to the Shorthorn breed in 1870 and 50 per cent relative to the foundation animals entered in the very first volumes of the Coates Herd Book. If their pedigrees could be traced back to the time when they had ancestors in common with other bovine breeds or races, it

might possibly be found for example, that they are probably alike in 70 per cent of the genes which would be different in random pairs of cattle from a population which included all cattle now living in Europe. No practical purpose would be served by tracing pedigrees that far; but the example may explain the apparent inconsistencies which occur when we compare relationships between members of the same breed, between animals of mixed breeding, or between animals belonging to different breeds or even to different species. The apparent inconsistencies arise because the populations chosen as bases for computing the relationships are not the same. The inconsistency is no more a real one than if we say that a certain mountain peak is 2,500 feet above the plane at its base but 12,000 feet above sea level. The height of the peak is the same in either case—the two figures differ merely because the base from which the height is measured is different in the two cases.

The processes of computing relationship do not allow for changes which mutation and selection may have caused in gene frequency. The errors caused by neglecting mutation are not serious unless the base for relationship was hundreds of generations in the past. Those caused by neglecting selection might be important for genes with major effects and under intense selection even when the base date is as recent as six or eight generations in the past. This is additional reason for not computing relationships to a distant base date. Instead one considers what the breed or race average was at a fairly recent date, how it differed from the average of other breeds, etc., and then considers the two related individuals in terms of how like each other they probably are in genes which would have been different in animals descended from the same breed or race at the base date but without ancestors in common since.

If two animals are related to an extent which is worth knowing for practical purposes (i.e., in addition to knowing whether they are members of the same breed), that relationship will usually come from ancestors not more than four or five generations back in the pedigrees of either. Even where there is some reason to express relationship relative to a more distant base, it is usually sufficient to trace the pedigree to a date about four or five generations back and then to assume that the ancestors at that time were a random sample of the breed. For example, in a study³ of Holstein-Friesians born in 1909 these were found to be related to each other about 2.6 per cent relative to the foundation stock of about 1883. If a present-day Holstein-Friesian is related 40 per cent to another, both pedigrees being traced back only to 1909, we are not

³ Lush, Jay L., Holbert, J. C., and Willham, O. S. 1936. Genetic history of the Holstein-Friesian cattle in the United States. *Jour. of Heredity*, 27:61-72.

apt to be seriously in error if we assume that the relationship found if both were traced back to 1883 would be about 41.6 per cent (40 per cent plus 2.6 per cent of the remaining 60 per cent). In other words, 40 per cent relative to 1909 is about the same as 41.6 per cent relative to 1883 in this breed.

In human relationships it is usually convenient to assume that the foundation ancestors in the two pedigrees being compared were random samples from the same population. This may lead to some discrepancies in a population like that of the United States, where some individuals are descended entirely from ancestors coming from one race while others are descended from crosses between two or more rather distinct races. People of the same race might consider themselves unrelated and yet on the average be alike in more of their genes than two first cousins who come from a racial mixture. If pedigrees were known as far back as the time when the races originally diverged from each other, the figures for human relationship would be reasonably consistent also, except for changes produced by mutation and natural selection and accumulated chance variations since the races ceased to intermarry freely. But human pedigrees are not known that far. Many people would have difficulty in even naming all eight of their great grandparents.

THE MEASUREMENT OF RELATIONSHIP

Measuring relationship is evaluating the probability that the two related individuals will have duplicate genes because they are related by descent. Each line or path of relationship is evaluated separately. The results are then added to get the total probability of likeness in their genes. It is often convenient to separate direct relationship and collateral relationship in the computations, although a given percentage of relationship represents the same probability of genetic likeness, regardless of whether it is collateral or direct. Direct relationship is that which comes about because one animal is the ancestor of the other, as parent and offspring or grandsire and grandson. Collateral relationship is that which comes about because both animals are descended in part from some of the same ancestors, as half and full brothers, uncle and niece, cousins, etc.

The first thing to do is to examine the pedigrees and find all the paths or lines of descent by which the two animals are related. To evaluate the closest paths first is usually more convenient and less likely to lead to duplication or omissions. Usually two individuals are not connected by many different paths of relationship unless there has been some inbreeding.

Direct relationship is measured by what animal breeders commonly

call "percentage of blood." By "blood" is meant inheritance in general or the genes considered collectively. The physical substance, blood, is not actually transmitted from parent to offspring at all. The young embryo makes its own blood. Figure 29 shows the percentages of "blood" arranged in the form of a pedigree. The fractions come naturally out of the halving nature of Mendelian segregation.

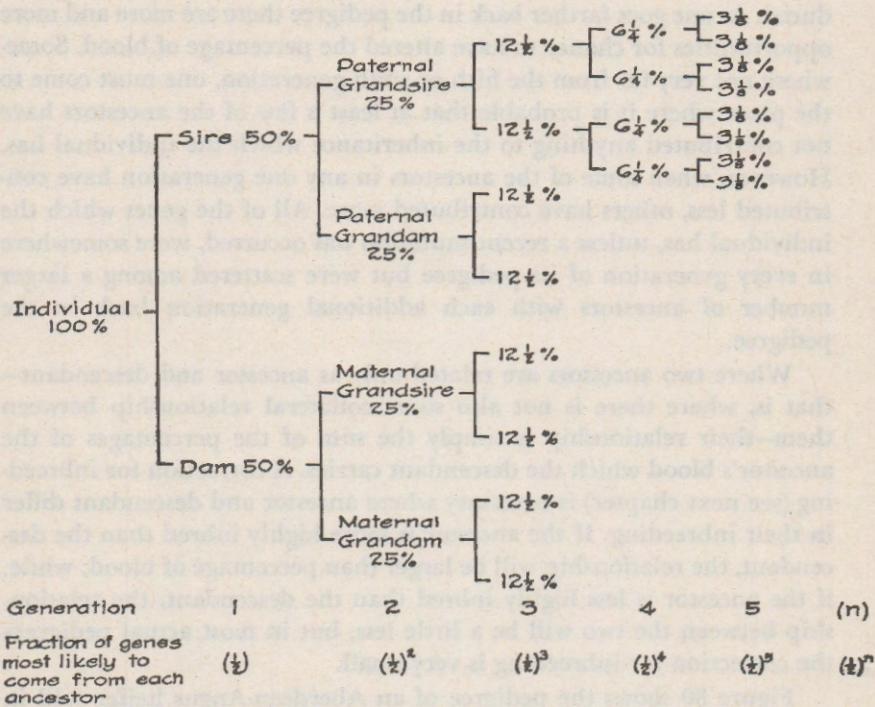


FIG. 29. The fraction of an individual's genes most likely to come from each ancestor.

The most probable proportion of an individual's genes to come from each of its ancestors is 50 per cent from a parent, 25 per cent from a grandparent, $12\frac{1}{2}$ per cent from a great grandparent, and so on, the percentage being halved with each additional generation the ancestor is farther back in the pedigree. Because of the part chance plays in Mendelian inheritance, these percentages need not be exact for an ancestor farther back than a parent. So far as concerns any one great, great, great grandparent, the most probable expectation is that the individual will have inherited $1/32$ of all its genes from that ancestor. Even in animals having 30 pairs of chromosomes, this does not average quite two chromosomes from each ancestor in that generation. Since there is

some crossing-over, it is probable that the individual will still have at least a few genes from every ancestor in that generation. However, it could happen that certain ancestors in that generation would have contributed nothing at all to this individual's inheritance. So far as concerns the inheritance which the descendant has, such ancestors might as well never have existed except that they were a part of the living machinery without which this individual would not have been produced. As one goes farther back in the pedigree there are more and more opportunities for chance to have altered the percentage of blood. Somewhere not very far from the fifth or sixth generation, one must come to the place where it is probable that at least a few of the ancestors have not contributed anything to the inheritance which the individual has. However, when some of the ancestors in any one generation have contributed less, others have contributed more. All of the genes which the individual has, unless a recent mutation has occurred, were somewhere in every generation of its pedigree but were scattered among a larger number of ancestors with each additional generation back in the pedigree.

Where two ancestors are related only as ancestor and descendant—that is, where there is not also some collateral relationship between them—their relationship is simply the sum of the percentages of the ancestor's blood which the descendant carries. A correction for inbreeding (see next chapter) is necessary where ancestor and descendant differ in their inbreeding. If the ancestor is more highly inbred than the descendant, the relationship will be larger than percentage of blood; while, if the ancestor is less highly inbred than the descendant, the relationship between the two will be a little less, but in most actual pedigrees the correction for inbreeding is very small.

Figure 30 shows the pedigree of an Aberdeen-Angus heifer sold in 1931 in the Strathmore sale. This heifer "carries 81 $\frac{1}{4}$ per cent of the blood of" Earl Marshall. This figure is the sum of: 25 per cent for each of Earl Marshall's two appearances as grandsire, 12 $\frac{1}{2}$ per cent for each of his two appearances as great grandsire, and 6 $\frac{1}{4}$ per cent for his one appearance as great great grandsire in this pedigree. By similar computations it will be seen that Earl Marshall 50th carries 87 $\frac{1}{2}$ per cent of the blood of Earl Marshall and that Blackcap Empress 74th carries 75 per cent of the blood of Earl Marshall. The percentage of Earl Marshall blood in the daughter is naturally the average of that in her parents. These figures for percentage of blood need only a small correction for inbreeding (larger than usual in this case) to become the coefficients of relationship of Earl Marshall to these three descendants of his.

Collateral relationship between two animals is computed separately

for each line of descent by which it is possible to go from one of them back to the common ancestor and then down to the other. Each generation in this line of descent is another Mendelian segregation halving the fraction of genes which are likely to be duplicates in the two animals because of their common descent. If there are many more than four or

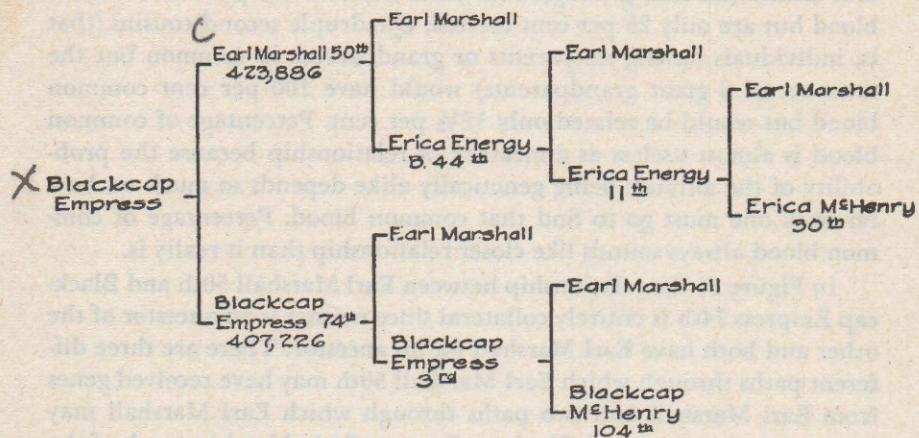


FIG. 30. A pedigree showing high relationship to the Aberdeen-Angus bull, Earl Marshall.

five intervening segregations, the amount of relationship through any one such line will be insignificantly small; but if there are many such lines, their total may be large enough to be of some importance.

The probability that cousins will have the same genes may be computed by extending the same process used for computing the relationship between half brothers. For each pair of genes the chance is one-half that a grandparent will give the same gene to both its offspring. Only one-half the times when this does happen will this same gene be transmitted to the one cousin. In only one-half of those cases will the other offspring transmit the same gene to the other cousin. There is, therefore, one chance in eight that an identical gene shall reach two cousins from a common grandparent. Even this concerns only half of their inheritance, since the other half comes from their other parent. Hence the probable genetic likeness between cousins on account of common descent from one grandparent is that $1/16$ of their genes will be identical because of this. If, as is usually the case with human first cousins, they have two grandparents in common, this adds an equal probability of their having the same genes through descent from that other grandparent. This makes a total probability that $1/8$ of their genes will be alike because of the common ancestry, while the rest of their genes are

no more and no less apt to be alike than if they were unrelated members of the same freely interbreeding population.

Breeders sometimes measure collateral relationship by "percentage of common blood," but this can be very misleading. Full brothers have 100 per cent common blood but are only 50 per cent related; double first cousins (all four grandparents the same) have 100 per cent common blood but are only 25 per cent related. Quadruple second cousins (that is, individuals having no parents or grandparents in common but the same set of 8 great grandparents) would have 100 per cent common blood but would be related only 12½ per cent. Percentage of common blood is almost useless as a measure of relationship because the probability of the animals being genetically alike depends so much on how far back one must go to find that common blood. Percentage of common blood always sounds like closer relationship than it really is.

In Figure 30 the relationship between Earl Marshall 50th and Blackcap Empress 74th is entirely collateral since neither is an ancestor of the other and both have Earl Marshall for an ancestor. There are three different paths through which Earl Marshall 50th may have received genes from Earl Marshall and two paths through which Earl Marshall may have transmitted genes to Blackcap Empress 74th. Matching each of the three ways with each of the two ways makes six different ways in which these two descendants of Earl Marshall might have received duplicates of any gene which was in him. The fact that Earl Marshall is the sire of both contributes 25 per cent to their relationship. The two different ways in which he is the sire of one and the grandsire of the other contribute 12½ per cent each. Descent from him as grandsire on both sides contributes 6¼ per cent. Descent from him as sire of one and great grandsire of the other contributes another 6¼ per cent. Finally the small probability that these two animals would get identical genes by the long route from Earl Marshall as great grandsire of one and grandsire of the other contributes another 3⅛ per cent to their relationship. This makes a total of 65% per cent, all of it coming through their descent from Earl Marshall, but that is still to be corrected for their inbreeding. A somewhat simpler way of figuring their relationship in this case, where they have only one ancestor in common, is to find that one of them has 75 per cent of the blood of Earl Marshall, while the other has 87½ per cent, and to multiply those two percentages together. This method gives the same answer; but if the two animals had more than one ancestor in common, the computations would have to be made separately for each such ancestor. This method will lead to difficulties if the common ancestors are related to each other.

These rules for computing relationships are nothing but counting

the number of Mendelian segregations which have intervened in each line of descent connecting two individuals, and using $(\frac{1}{2})^n$ as the fraction of their genes which are likely to be identical because the two animals received duplicate genes in that way from their common ancestor.

When one animal is an ancestor of the other and they are also related collaterally because both are descended from a third animal, it is usually more convenient to compute the direct relationship first. An example of this can be had from Figure 30 if we wish to learn how closely Earl Marshall 50th is related to his daughter, Blackcap Empress. They are directly related as sire and daughter, and in addition he may have received from Earl Marshall some genes for which she received duplicates through her dam. He traces to Earl Marshall in three different lines, the number of generations in each being 1, 2, 3, respectively, while she traces through her dam to Earl Marshall in two lines, the number of generations being 2 and 3 in those. Combination of each of the two with each of the three makes six different ways in which these two animals may have received duplicate genes by descent from Earl Marshall. The sum of the separate values for these six paths equals $32 \frac{13}{16}$ per cent collateral relationship to be added to the 50 per cent direct relationship. That total is still to be corrected for the inbreeding, which in this case is intense enough to make that correction rather large.

Figure 31 shows another example. The relationship of X to A is both direct and collateral, while the relationship between X and Z is entirely collateral, neither being an ancestor of the other. The arrow diagram of the pedigree is often very convenient for showing at a glance the nature of the relationship. If the pedigrees are complicated by much inbreeding, the arrow diagram is almost necessary in order not to omit some lines of relationship nor count some a second time without being aware of having done so. The relationship of X to Z in Figure 31 will illustrate why percentage of common blood is not dependable as a measure of collateral relationship. It is not legitimate to say that 75 per cent of X's blood is the same as 100 per cent of Z's blood and to estimate their relationship through manipulating these figures of "common blood" in any way. It is legitimate to do this separately for each common ancestor and to say that Z has 50 per cent of the blood of D and X has 25 per cent of that blood and that Z and X are therefore related 50 per cent of 25 per cent, or $12\frac{1}{2}$ per cent, through D. Also, it is legitimate to say that both Z and X have 50 per cent of the blood of C and that 50 per cent of 50 per cent equals 25 per cent of relationship between Z and X through descent from C. This 25 per cent may then be added to the $12\frac{1}{2}$ per cent of relationship through D to give the total relationship of $37\frac{1}{2}$ per cent.

Relationship between two individuals cannot be higher than 50 per cent unless some inbreeding has been practiced. The only exception to this concerns identical twins, and members of the same "clone" in plants and animals which can be propagated asexually. Relationship between members of such isogenic lines is 100 per cent, since they are

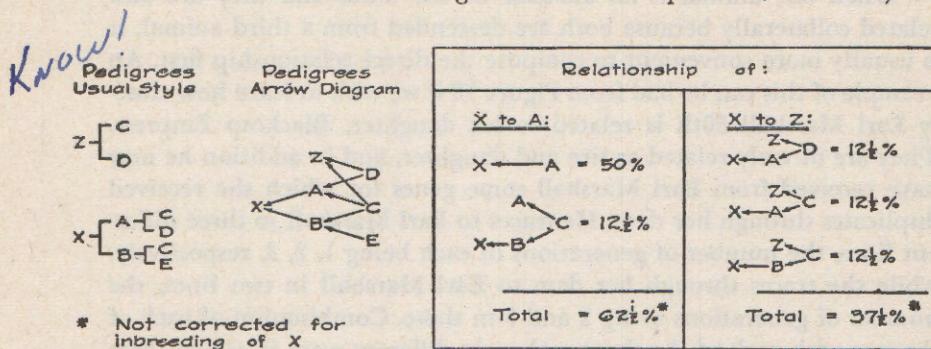


FIG. 31. Showing how relationship is computed.

really duplicates of the same zygote and there has been no intervening Mendelian segregation or recombination to permit them to have unlike genes. Since not much inbreeding occurs in most animal species or in man, we rarely have a chance to see the resemblance between animals related much more closely than 50 per cent. It is largely for this reason that identical twins are such interesting evidence about the importance of heredity. An increase from 50 to 100 per cent in genetic likeness makes a marked difference in the variation to be expected between individuals, especially in characteristics which are highly hereditary.

Two animals cannot be very closely related if all their common ancestors are distant ones. Rarely is much gained by going back farther than three or four generations in the pedigrees of two animals to see whether they are related. In an extreme case two animals might have the very same 16 great great grandparents, and yet their relationship to each other would be only $6\frac{1}{4}$ per cent if they had no parents, grandparents, or great grandparents in common and if there were no inbreeding involved.

Relationship is sometimes measured in "degrees," especially for legal purposes. In civil law a degree of relationship corresponds to a generation of Mendelian segregation. Thus parent and offspring are "related in the first degree," grandparent and offspring are "related in the second degree," uncle and nephew are "related in the third degree," etc. When the individuals are related through more than one line of descent, each line is computed and stated separately without combina-

tion into a single figure. In canon law and common law only the number of generations in the longer line of descent from the common ancestor is counted. Thus uncle and nephew are related in the second degree by canon law and common law.

THE EFFECTS OF SEX-LINKAGE

In the mammals the male is the heterogametic sex. His sex-linked inheritance comes entirely from his mother. Her sex-linked inheritance is present in duplicate, and among the pairs of sex-linked genes which are heterozygous in her, chance at segregation determines what sex-linked inheritance a son shall receive. The result is that 100 per cent of his sex-linked genes are like 50 per cent of hers. The square root of the product of these is the relationship (71 per cent) of son and dam for sex-linked genes. The sex-linked inheritance of a female comes equally from both parents; but since her sire does not have a duplicate set of sex-linked genes, chance plays no part in determining what sex-linked inheritance she shall receive from him. So far as his daughters are concerned, the situation is the same as if the sire were homozygous for all his sex-linked genes. The relationship between sire and daughter is also 71 per cent for sex-linked genes, since 100 per cent of those in the sire are like 50 per cent of those in his daughter. Daughter and dam are related 50 per cent for sex-linked genes, just as they are for autosomal genes. Sire and son are not related at all for sex-linked genes, since the son cannot receive any of those from his sire. The practical consequence of sex-linkage is to make the parent-offspring relationship higher between opposite sexes than it is between parent and offspring of the same sex. In birds, moths, and some fishes the female is heterogametic, but that leaves the practical situation nearly the same: namely, that males are a bit more closely related to their dams and females to their sires than either is to the parent which is the same sex. The lowest relationship for sex-linked genes is that between sire and son in the mammals, but between dam and daughter in birds.

This difference in relationship to ancestors of different sexes is partially, but not entirely, equalized as one goes further back in the pedigree, since a dam may transmit either the sex-linked genes she got from her sire or the sex-linked genes she got from her dam.

Since the farm animals have about 20 to 30 pairs of chromosomes and only one pair carries the sex-linked genes, it is improbable that the total amount of sex-linked inheritance is much larger than 3 to 5 per cent of the total inheritance. Hence, for practical purposes no material error is introduced by neglecting sex-linkage when computing relationships. (See table 20.) Occasionally there may be individual matings in which sex-linkage will play a noticeable part.

PRACTICAL USES OF THE RELATIONSHIP COEFFICIENT

The most important practical use of the relationship coefficient is to predict the merit of relatives of animals whose merit is known. This is the whole basis for using the merit of relatives to aid in making selection more effective. If nothing at all is known about an animal or its relatives, the only prediction we can make is that it will be an average animal of its breed. Neglecting for the moment the effects of environment, dominance, epistasis, and selection, if we know an animal related 40 per cent to the unknown one, the most probable prediction is that the unknown animal will deviate from the breed average in the same direction as the known relative does, but only 40 per cent as far. If a cow's genotype for fat production is 100 pounds above the breed average the most probable genotype of her daughter, if nothing is known about the sire except that he belonged to the same breed, is that the daughter's genotype will be 50 pounds above the breed average. Numerous practical difficulties and necessary precautions beset this use of relationship as a measure of how much weight to put on each relative in estimating the breeding worth of an animal. Most of those hinge around the inescapable fact that we are not sure of the genotypes of the relatives but only know their apparent merit. The two may be widely different if outward merit is much affected by environment, dominance, or epistasis. Other difficulties concern the weight to give each relative in combining information about several related ones, not all known equally well, into the best single estimate of what the unknown animal will be. The practical aspects of this were discussed in chapter 14. They put serious limitations on the practical usefulness of the principle—which is true when comparing equally well-known relatives of which one is to be used alone in such estimates—that the attention to be given such relatives is in proportion to their relationship to the animal to be estimated. The relationship between an individual and the average genotype of a group of its relatives may be higher than its relationship to any one of them. The simplest and most important example of this is the case of half sibs. In the extreme case of a characteristic perfectly hereditary in the simple additive way, and unselected half sibs from a random breeding population, the equation for predicting with the least error what an individual will be from knowing p of its paternal half sibs and m of its maternal half sibs is:

$$\begin{aligned} \text{Animal} = & \text{breed average} + \frac{p}{p+3} (\text{paternal half sibs minus breed} \\ & \quad \text{average}) \\ & + \frac{m}{m+3} (\text{maternal half sibs minus breed} \\ & \quad \text{average}) \end{aligned}$$

As p and m increase from one to at least four or five, the usefulness of this equation goes up rapidly and it soon comes close to the limit set by perfect knowledge of the genotypes of sire and dam of the individual being predicted. Of course, in actual practice there are effects of environment and dominance and epistasis and possible previous selection of half sibs which will usually make it wise to put less weight than this on what the half sibs indicate. The above equation shows quantitatively what we are recommending if we advise choosing a son of a proved sire and a proved dam.

To the extent that the trait being measured is affected by environment, dominance, and epistasis, actually observed likeness will be less than the genetic likeness unless each pair of related individuals tended to be exposed to an environment alike for them but different from the environment of other pairs. In that case the observed may be higher than the calculated. Thus, in a random bred population half sisters are genetically as much alike as grandam and granddaughter; but each pair of half sisters is more apt to have been exposed to the same more or less unusual environment than is each grandam and granddaughter pair. Hence, in such data as official dairy records, it is to be expected that the observed likeness between half sisters will be larger than that between grandam and granddaughter. For the same reason paternal half sisters, which are usually contemporaries, may be expected actually to resemble each other a little more closely than maternal half sisters. The latter may have been born and reared several years apart.

Dominance and epistasis make observed likenesses generally lower than calculated ones, but in certain relationships—of which the most important is that between full sibs—dominance produces a little extra likeness on its own account. This partly offsets its general tendency to lower likenesses.

If breeders' ideals diverge enough that they have been selecting for distinctly different types within the same breed, then animals in the same herd are apt to resemble each other, relative to the whole breed, more than their relationships indicate.

GALTON'S LAW

Two distinct although related ideas are sometimes confused under the name "Galton's Law." The first is the observed fact that the correlation between parent and offspring is nearly + .50 in populations where there is not much inbreeding and where the trait being measured is highly hereditary. The correlation between an animal and a more remote ancestor is halved for each additional generation which separates them. This is precisely what was shown in Figure 29 and was dis-

cussed under "percentage of blood." It was an observed fact in Galton's time and had been used by practical breeders in England from at least as long ago as 1815.⁴ The only material difference now is that we understand why it is a natural consequence of the laws of inheritance, provided the population is mating at random and the trait being studied is entirely hereditary in the simple additive manner. Naturally the extent to which these conditions are fulfilled varies in different populations and even for different traits in the same population and often is known only within rather wide limits.

The other part of Galton's law—which unfortunately is the part most frequently quoted—is true only in a specialized statistical sense. The square of the correlation coefficient measures the portion of the variance in one variable which disappears in data in which the other variable is constant. In this special statistical sense the individual's inheritance is $\frac{1}{4}$ determined by its sire and $\frac{1}{4}$ by its dam. That instantly raises the question: What determines the remaining $\frac{1}{2}$? Galton reasoned that this same process would be repeated with the sire and with the dam, each of them being $\frac{1}{4}$ determined by its sire and another $\frac{1}{4}$ by its dam, and that if this process were pursued far enough the fractions would ultimately add up to one. Consequently he proposed as a general "law" that the individual's inheritance was $\frac{1}{4}$ determined by its sire and $\frac{1}{4}$ by its dam, $1/16$ by each of the four grandparents, $1/64$ by each of the 8 great grandparents, and so on, each ancestor contributing just $\frac{1}{4}$ as much to the total inheritance as did the one a generation nearer to the individual. This is usually pictured as in A, of Figure 32. Because this seemed a logical scheme, it was accepted rather widely and even today is sometimes quoted with approval. Unfortunately, the obvious inference from this diagram (that if one knew all about all of the ancestors, he would know all about the heredity of this individual) is not true.

Had Galton used multiple correlation technique (as Yule pointed out at the third International Genetics Congress in 1906) he would have found that the partial correlation between grandparent and grandson or granddaughter, the intervening parent being held constant, is zero in any population in which the correlation between parent and offspring is .50 and the correlation between grandparent and grandson or granddaughter is .25. If the parent's heredity is not known, it is still true in the technical statistical sense of the word that the individual is "determined" $1/16$ by each of its grandparents. That is shown for the paternal grandam by D in Figure 32. But if the parent's heredity is known, knowledge of the grandparents adds nothing to the

⁴ According to the encyclopedia of J. G. Krünitz.

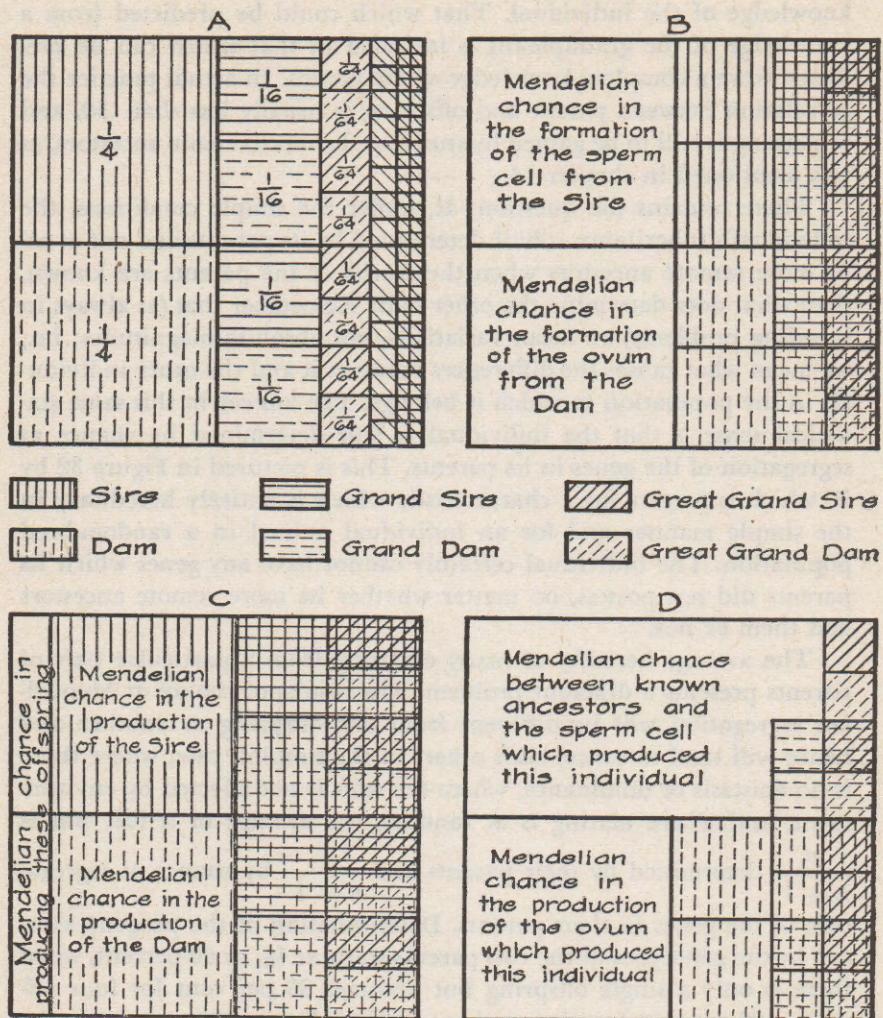


FIG. 32. Galton's "law" of the relative importance of various ancestors, pictured for a characteristic perfectly hereditary in the simple additive way. *A*: As formulated by Galton, each ancestor being considered singly. *B*: Correctly pictured for an individual animal in a random breeding population. That which can be predicted from the more remote ancestors is included in what can be predicted from the intervening ancestors. Mendelian chance at segregation accounts for half of the determination in the statistical sense of that word. *C*: Same as *B* except that this concerns the average inheritance of nine unselected offspring from one pair of parents. The effects of chance in the nine segregations which produced the sperm cells and in the nine segregations which produced the ova tend to cancel each other to such an extent that Mendelian chance now determines only one-tenth of the average inheritance of these nine instead of the one-half which it determines for each individual. *D*: Determination of the individual by known characteristics of its ancestors in the case where males cannot express the characteristic themselves and neither the sire nor the two grandsires were progeny-tested.

knowledge of the individual. That which could be predicted from a knowledge of the grandparent is included in that which can be predicted from a complete knowledge of the parent. In actual practice the correlation between parent and offspring is usually less than .50, and something is still to be gained by studying the more remote ancestors, as was mentioned in chapter 14.

There remains the question: If, under the simple conditions, the individual's inheritance is half determined by its parents and not at all by more remote ancestors when the merits of the parents are known, then what does determine the other half? Remember that (as always in breeding problems) we mean variations, not absolute magnitudes; i.e., we mean what causes the differences between it and the other individuals in the population to which it belongs. The answer in this same statistical sense is that the individual is half determined by chance at segregation of the genes in its parents. This is pictured in Figure 32 by B, which is correct for a characteristic which is entirely hereditary in the simple manner and for an individual animal in a random-bred population. The individual certainly cannot have any genes which its parents did not possess, no matter whether its more remote ancestors had them or not.

The average heredity of many offspring from a particular pair of parents presents a different problem. The results of chance at Mendelian segregation will be different from one offspring to another and hence will tend to cancel each other. In the simplest case, where there is no epistasis or dominance, where the trait is not affected by environment, and where mating is at random, the average of n full sibs is

$\frac{n}{n+1}$ determined by their parents and $\frac{1}{n+1}$ by chance at segrega-

tion of the genes in their parents. Determination of the progeny average by the genotypes of the two parents starts at $\frac{1}{2}$, or 50 percent, when there is only a single offspring but becomes 80 per cent for four offspring, 90 per cent for nine, and approaches close to 100 per cent as the numbers of offspring become very large. This is pictured in C of Figure 32 for the case where $n = 9$. This is why complete knowledge of the genotypes of the parents would permit predicting with almost perfect accuracy what the average of their progeny (if numerous) will be, even though it would not permit highly accurate prediction of what each individual offspring will be. D of Figure 32 shows Galton's law when the merits of some of the near ancestors on one side of the pedigree are not known.

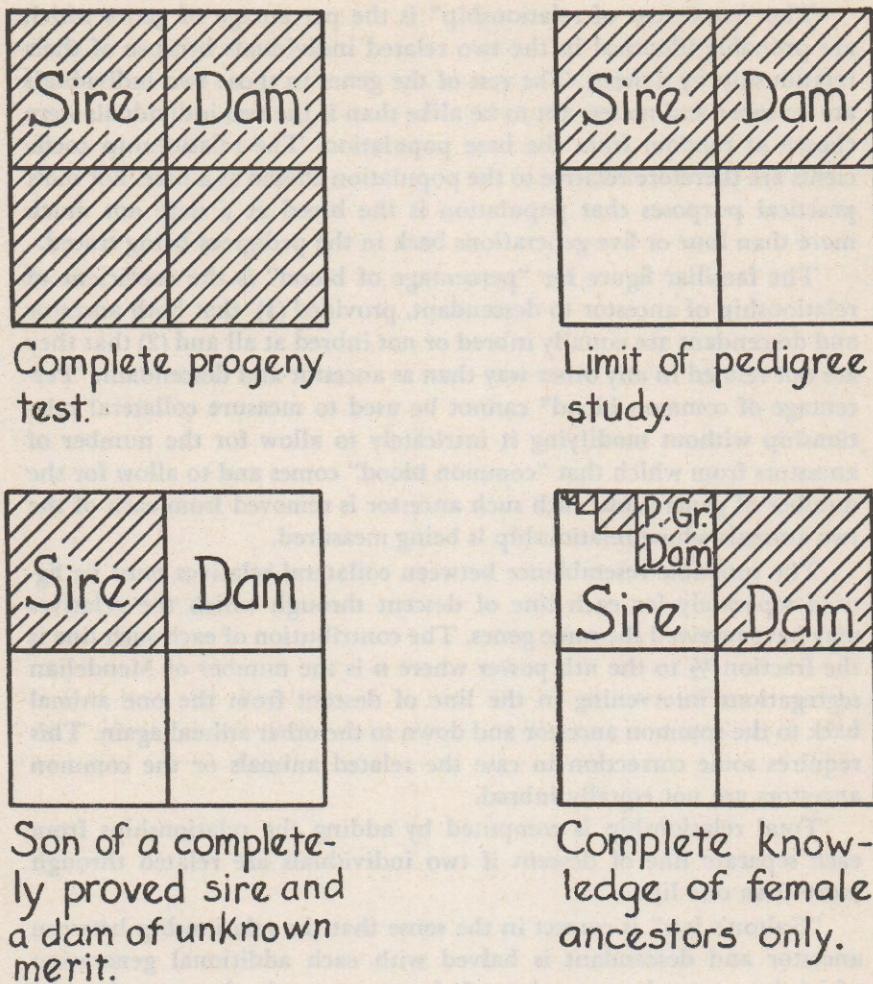


FIG. 33. Relative accuracy of a progeny test and of various kinds of pedigrees when the information in each is as complete as is theoretically possible under the conditions named. Shaded areas represent portions of the individual's inheritance determined (in the statistical sense) by complete information of the kind pictured. The correlation between the actual and the predicted breeding value of the individual would be the square root of the shaded fraction of the area; i.e., 1.0 in the upper lefthand corner, .71 in the upper right, .50 in the lower left, and .58 in the lower right. The unshaded areas represent possibilities for Mendelian segregation to have made the individual's actual breeding value higher or lower than its expected breeding value.

SUMMARY

The genetic resemblance between individuals is based on the probability that they have received identical genes from animals which are ancestors of them both.

The "coefficient of relationship" is the percentage of genes which are probably identical in the two related individuals because of their relationship by descent. The rest of the genes in those two individuals are no more and no less apt to be alike than if the two individuals were chosen at random from the base population. The relationship coefficients are therefore relative to the population chosen as a base. For most practical purposes that population is the breed at a date not much more than four or five generations back in the pedigrees being traced.

The familiar figure for "percentage of blood" is the coefficient of relationship of ancestor to descendant, provided (1) that both ancestor and descendant are equally inbred or not inbred at all and (2) that they are not related in any other way than as ancestor and descendant. "Percentage of common blood" cannot be used to measure collateral relationship without modifying it intricately to allow for the number of ancestors from which that "common blood" comes and to allow for the number of generations each such ancestor is removed from each of the two animals whose relationship is being measured.

The probable resemblance between collateral relatives must be figured separately for each line of descent through which the relatives may have received the same genes. The contribution of each such line is the fraction $\frac{1}{2}$ to the n th power where n is the number of Mendelian segregations intervening in the line of descent from the one animal back to the common ancestor and down to the other animal again. This requires some correction in case the related animals or the common ancestors are not equally inbred.

Total relationship is computed by adding the relationships from each separate line of descent if two individuals are related through more than one line.

"Galton's law" is correct in the sense that the relationship between ancestor and descendant is halved with each additional generation which intervenes between them. It is not correct in the sense that the individual's heredity is completely determined by the heredity of its ancestors. In that sense in a random-bred population the individual is one-fourth determined by each parent and one-half determined by chance in Mendelian segregation. Determination by more remote ancestors is included in the determination by the parent.

The existence of sex-linkage causes sons to resemble dams a little more than they do their sires and makes daughters resemble their sires a bit more closely than they do their dams. This effect must be small in most cases.

Relationship measures the probability that individuals will be alike *in their genes*. Their actual outward likeness depends also upon how

much the traits being measured are affected by environment, dominance, and epistasis, upon the extent to which their environments were correlated, and upon whether their ancestors were mated like to like.

The most important practical use for relationships is in predicting the most probable merit of unknown or perhaps even unborn individuals from the merit of their known relatives.

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CHAPTER 21

The Consequences and Measurement of Inbreeding

Inbreeding is the mating of closely related animals. Everyone agrees to that general definition, but there is much diversity of usage about how closely related the mates must be before the mating should be called inbreeding. Many practical breeders restrict the word inbreeding to the mating of full brother and sister or of parent and offspring. Others would call the mating of half brother and sister, or the mating of grandparent to grandson or granddaughter inbreeding. The broad scientific definition is that inbreeding is the mating of animals more closely related to each other than the average relationship within the population concerned. Such matings tend to make the offspring more homozygous than if their parents were of average relationship to each other. Mating of animals less closely related than the average of the population concerned is outbreeding.

The population concerned would usually be the whole breed when this definition is applied to animal breeding, but might be the race or the whole species when considering the part which inbreeding may play in evolution. The intensity of the inbreeding is very slight, however, unless the mates are quite closely related or the inbreeding is continued for many generations. This leads to the convenient situation that the great majority of all breedings which take place within a pure breed are practically neutral so far as any inbreeding or outbreeding effect is concerned and may be classed as random breeding, even though one does not know the average relationship within the breed. The practical use of the definition that inbreeding is the mating of closely related animals merely requires agreement as to how close that relationship must be.

It is impossible to define inbreeding simply as the mating of related animals. All animals that can be mated at all are related, at least slightly. Each individual has two parents, four grandparents, eight great grandparents, and so on, the number of ancestors doubling each generation. In the tenth generation of its pedigree an animal will have more than a thousand ancestors if there has been no inbreeding. If two ani-