

tency. Every offspring which receives a dominant gene will show the effect of that gene. If the gene is completely dominant and the parent is homozygous for it, then all of the offspring will appear exactly alike for the effect of that gene, regardless of the inheritance they received from the other parent. When a parent having many dominant genes is also highly homozygous, its prepotency is maximum.

A breed which has several conspicuous dominant traits will appear to be prepotent in crosses with other breeds. This does not mean that it will be prepotent in other characteristics. For example, crossing of Herefords with Aberdeen-Angus ordinarily produces white-faced, black animals without horns. In this case the Angus breed is prepotent for body color and for the absence of horns, but the Hereford breed is prepotent for the white face. Body color and the presence or absence of horns are conspicuous characteristics. One who does not examine the animals carefully might infer that prepotency is a general characteristic of the animal as a whole. Probably most statements that a certain animal transmitted all of its qualities uniformly to all of its offspring are based on careless observation of an animal which was homozygous for one or a few conspicuous dominant traits. To the man unfamiliar with Aberdeen-Angus cattle the mere fact that a group of cattle are hornless and black would make them seem impressively alike to him. But the man familiar with black-polled cattle would be looking for other things and would not be much impressed by this.

Linkage has the general effect of making most of the offspring of an individual fall into a smaller number of classes than if there were no linkage. If there has been considerable selection among the offspring of that animal, many having been discarded before we see them, linkage may thus give us the impression of more prepotency than we would have observed if all the genes had been segregating independently.

Epistasis may sometimes add something to apparent prepotency. Occasionally a sire will be homozygous for one or more genes which, when brought together with genes which many of his mates have, will produce conspicuous results, although the genes may have little apparent effect when the full combination is not present. As a result the offspring from such a sire will be unusually like each other and yet distinctly different from either their sire or their dam. It is not certain whether this happens often, but it is a possibility and is the most plausible genetic explanation for some cases reported.

THE MEASUREMENT OF PREPOTENCY

After the offspring are produced, there are two ways of measuring prepotency. The first is to measure directly the resemblance of this ani-

mal and its offspring, as compared with the usual resemblance of parent and offspring. The second is to measure how closely the offspring of this sire resemble each other, as compared with the usual resemblance between half brothers and sisters. In the first method any permanent effect produced in the parent by environment, dominance, or epistasis will appear in every comparison of that parent with each of its offspring. Therefore, the second method is generally to be preferred. Moreover, the second method is the only one available in cases such as measuring a dairy bull's prepotency for milk and fat production, since he cannot himself express those traits. A weakness of the second method is that the offspring are more likely to have been exposed to the same peculiarities of environment than parent and offspring are. Thus if one bull's daughters freshened in a poorly managed herd and a second bull's daughters all freshened in a well-managed herd, a breeder knowing only the records and not about the difference in management is likely to conclude mistakenly that the first bull was prepotent for low production and the second bull was prepotent for high production. Also, the second method will give a high figure for prepotency in those cases where the offspring resemble each other closely but are distinctly different from either parent, as might sometimes happen if there were much epistasis in a particular mating. Some breeders would not like to call such a sire prepotent, since the offspring do not resemble him even though they are unusually uniform.

Prepotency has its limits. In the absence of dominance and epistasis, the most prepotent sire in the world when mated to random-bred females cannot do more than make his offspring, which are half sibs, resemble each other as closely as ordinary full brothers and sisters from random-bred parents would. The relationship between half brothers

which are not themselves inbred is $\frac{1+F}{4}$, where F is the inbreeding

coefficient of their common parent. This relationship is only one-fourth if the common parent is not inbred, but approaches one-half as F approaches 1.0. Now, if the genes of the common sire were all dominant in addition to being perfectly homozygous, we might have the appearance of still greater prepotency than this. The general effect of epistasis would be lower prepotency, since not all of the dams to which the sire was mated would have the genes necessary to nick well with those the sire carried. In exceptional cases epistasis might increase rather than decrease prepotency.

THE BREEDER'S CONTROL OVER PREPOTENCY

Dominance and epistasis result from the physiology and chemistry

of the genes in their reactions with each other and with the environment in the growth of the individual. The breeder can do little or nothing to change them. Linkage is likewise not subject to the breeder's control.

The breeder's control over prepotency is limited to changes he can make in the homozygosity of his stock. For all practical purposes he changes homozygosity little except by inbreeding. The more highly inbred an individual is, the more apt it is to be homozygous for an unusual number of genes. The inbreeding coefficient is the best estimate which can be made of an individual's prepotency before that individual has actual offspring, by which its prepotency can be measured. Prepotency can be increased only a very little by the practice of mating like to like without inbreeding. The resemblance between parents and offspring is much increased by mating like to like, but when animals bred in this way are mated to unrelated or random individuals, they show only a little more prepotency than if they themselves had been random bred.

The increased prepotency of inbred animals has been known at least since Bakewell's time, but breeders do not generally pay much money for it in the sale ring. The inbred animal is usually less apt to be prepotent for its poor traits than for its good ones, but that is not always recognized. The undesired traits are more often recessive than dominant. Therefore, they are not apt to appear in the offspring of the inbred individual when it is mated to unrelated animals which do not show those undesired traits.

MYTHS ABOUT PREPOTENCY

Prepotency is not transmissible from parent to offspring as other characteristics may be, except insofar as it depends on dominance. No matter how homozygous a parent is, it cannot transmit that homozygosity to its offspring. Its offspring can be homozygous only if they receive the same genes from both parents. A high degree of homozygosity can be attained only by many generations of inbreeding but can be destroyed by a single generation of outbreeding. We sometimes read in animal breeding history of cases where there was an unbroken line of succession of noted sires from father to son and to grandson, and so on. The Baron's Pride line in Clydesdales is an example. Often the history of the case is accompanied by the inference or perhaps the outright statement that this sire transmitted prepotency to his sons and his grandsons. What really happens in such cases is that there is much selection in each generation, and to some extent each sire's mates are selected to be like him. As we look back on the breeding history, we note

that one sire was more popular and successful than any other of his generation, just as his sire and grandsire were; but we do not notice the large number of half brothers which were discarded in each generation while finding the leading sire of that generation. If a sire is thought to be better than any of his contemporaries, he is likely to be bred to better mates than they are, and more of his sons are likely to be tried as sires in prominent herds. It is not necessary to invoke prepotency to explain why the most prominent sire of one generation is sometimes the son of the most prominent sire of the preceding generation.

Nothing which is known of the mechanism of heredity justifies the belief that masculinity in a male or femininity in a female indicates prepotency. Those traits are desirable to the extent that they indicate normal sex instincts and normal health of the sex glands but there is no reason for thinking that they indicate prepotency.

SUMMARY

Prepotency is the ability of an animal to make its offspring resemble that parent and each other more closely than is usual.

The genetic basis for prepotency is the degree of homozygosity of the animal and whether its genes are prevailingly dominant or recessive. To a small extent linkage and epistasis may play some part.

Almost the only control the breeder has over prepotency is the extent to which he builds homozygosis into his animals by inbreeding.

Prepotency is not transmissible from parent to offspring except insofar as it depends on dominance. Masculinity or femininity in appearance probably has nothing to do with prepotency, although it may be desirable as an indication of normal ability to reproduce.

CHAPTER 23

Linebreeding

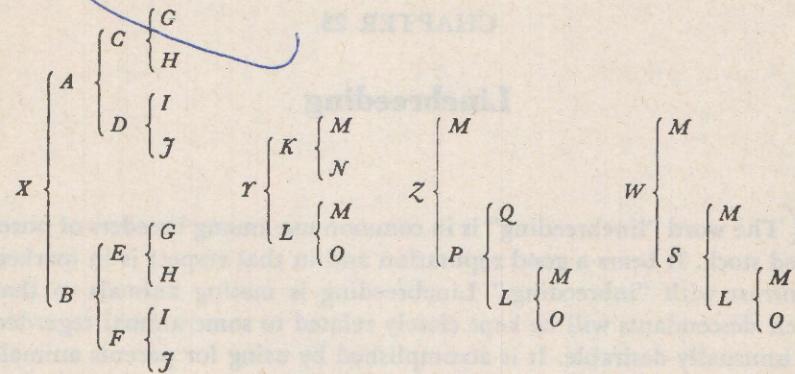
(The word "linebreeding" is in common use among breeders of purebred stock. It bears a good reputation and in that respect is in marked contrast with "inbreeding." Linebreeding is mating animals so that their descendants will be kept closely related to some animal regarded as unusually desirable. It is accomplished by using for parents animals which are both closely related to the admired ancestor but are little if at all related to each other through any other ancestors. If both parents are descended from the animal toward which the linebreeding is being directed, they are related to each other and their mating is a form of inbreeding in the broad sense of the word. If a man says an animal is linebred, this instantly calls forth the question: "Linebred to what?" In fact, he will not often make such an incomplete statement as that an animal "is linebred." He will say that this bull is "a linebred Domino" or these "are linebred Anxiety cattle" or "this bull is linebred to Prizemere 9th." The use of the term linebred almost carries with it the necessity of specifying the animal or group of closely related animals toward which the breeding is directed.

Linebreeding thus differs from other forms of inbreeding primarily in that it is directed toward maintaining a high relationship to some chosen ancestor and secondarily, in that it is usually less intense than the most extreme inbreeding which might be practiced. Relationship to the admired ancestor rather than intensity of inbreeding is dominating the breeder's thought when he uses the term linebreeding, even though this same breeder if he were asked for a formal definition of linebreeding might give one which would mention nothing but the intensity of the inbreeding.)

The pedigrees below show the difference between linebreeding and some other forms of inbreeding. The parents of *X* are double first cousins, having the same four grandparents. The parents of *Y* are half brother and sister. *Z* is produced by mating a male to his own granddaughter. *W* is produced by mating a sire to his daughter out of one of his own daughters. The intensity of the inbreeding is the same for *X*, *Y*,

Better known!
Behavioral

and Z. Yet X would rarely if ever be called linebred. Its sire and its dam are related through four different ancestors which, so far as the pedigree shows, may belong to four unrelated strains. If a breeder were to



call X linebred, he would have to say that it was linebred to four different lines at once, which is something of a contradiction in terms. He would call Y linebred to M because K and L are related only through M, and Y has been kept almost as closely related to M as its parents were. Z is even more clearly a case of linebreeding because it is more closely related to M than Y is, although no more intensely inbred. Many breeders would call W inbred instead of linebred because the intensity of its inbreeding is so high. Others would call it "intensely linebred to M," since all of its inbreeding is focused on M and it contains 87½ per cent of the blood of M—a relationship of 75 per cent after allowing for W's inbreeding.¹

WHY LINEBREEDING IS PRACTICED

Animals do not live long enough for the breeder to get all the sons and daughters he wants from the best ones. Often an animal is old or even dead before its real superiority is recognized. If its sons and daughters are mated to unrelated individuals, the offspring will get only about one-fourth of their inheritance from this outstanding grandparent. If these in turn are mated to unrelated individuals, the influence of the outstanding ancestor is again halved. Unless some form of linebreeding is practiced, it is only a matter of three or four generations until even the most outstanding animal's influence is so scattered and diluted that no one descendant is very much like it. Linebreeding takes advantage of the laws of probability as they affect Mendelian inheritance to hold the expected amount of inheritance from an admired

¹ For other illustrations see Iowa Agr. Exp. Sta., Bul. 301, *Linebreeding*.

ancestor at a nearly constant level instead of letting it be halved with each generation, as would happen if all the matings were outbreeding. Linebreeding provides, so to speak, a ratchet mechanism for holding any gains already made by selection, while attempting to make further gains.)

Linebreeding also builds up homozygosity and prepotency within the herd where it is practiced, just as other kinds of inbreeding do. It is no more effective than other forms of inbreeding in this respect except that, on account of the selection of the ancestors toward which the inbreeding is directed, the homozygosis produced by linebreeding is more apt to be for desired traits than is the case with undirected inbreeding. Linebreeding tends to separate the breed into distinct families, each closely related to some admired ancestor, between which effective selection can be practiced.

WHEN LINEBREEDING SHOULD BE PRACTICED

(The better the animals in a breeder's herd, the more reason he has for linebreeding to them. The most vulnerable part in the linebreeding program is whether the breeder is right when he decides which of the animals recently used in his herd really were extraordinarily good ones. If he can select the good from among the others with a high degree of accuracy, linebreeding will be a powerful tool in his hands. If his judgment about which animals were good is only fair, then linebreeding has only a little advantage over other forms of inbreeding.

Those who can best afford to linebreed are breeders whose herds or flocks are already distinctly superior to the general average of their breed. If, by wise choice or lucky chance, such a breeder has used on good dams a sire whose offspring turn out to be even better than their dams, such a breeder ought to linebreed at once and strongly to this sire while the animal is yet alive. If it is already dead when he discovers how good it was, then he should hasten to linebreed to it while it still has many sons and daughters by which such linebreeding can be accomplished. While an animal is still living, the possibility of producing offspring more closely related to it than any which yet exist remains open. If a sire is thought good enough to make the risk worth taking, he can be mated to his daughters and granddaughters generation after generation, as seems to have been the intention of those who bred Blackcap Empress (Figure 30). But after an animal dies the limit of relationship to it which can be attained in future animals is only that of its closest relatives then living. Even that is a limit only to be approached. If an animal is dead by the time we realize how good it was and if there are no living animals more closely related to it than 50 per cent, then there

is no possible way to produce animals more closely related to it than that. If we have let its sons and daughters and full brothers and sisters die before we wake up to its merit and there are left no living animals more closely related to it than 25 per cent, then we cannot produce any future animals more closely related to it than that—hence the importance of starting the linebreeding while there is time to do so effectively. Figure 39 shows a case where that seems to have been planned definitely.

It is an open question whether breeders with purebred herds of average merit can afford to do much linebreeding. Certainly there are many

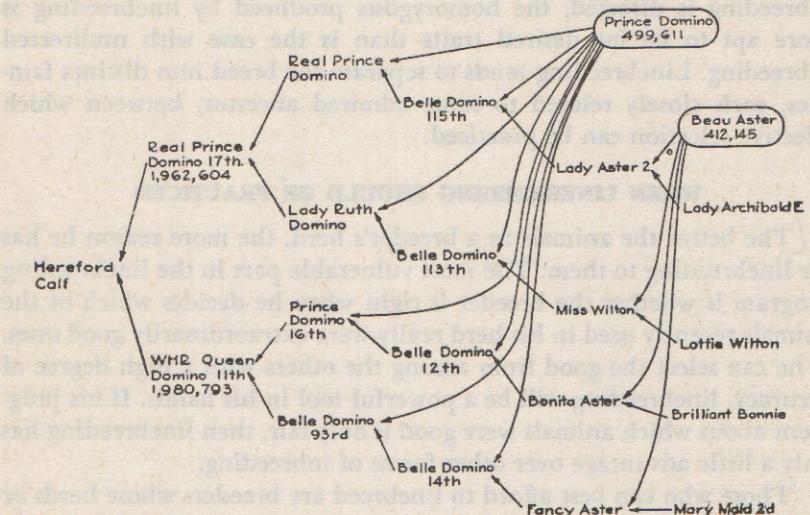


FIG. 89. Long-continued and deliberate linebreeding to Prince Domino with a very little linebreeding also to Beau Aster. Pedigrees like this do not "just happen." It took planning to get four different grandparents with so nearly identical pedigrees and to bring them together in this way without any secondary linebreeding.

good animals in such herds and much good inheritance which stands small chance of being kept together unless linebreeding is practiced. On the other hand, if the initial merit of the herd was only average, one must count on a certain amount of inbreeding degeneration which might bring the average merit of the herd below the level of the breed. The question at issue is whether the increased effectiveness of selection possible under linebreeding will be more than enough to offset the expected amount of inbreeding degeneration.

Breeders of grades cannot often afford to linebreed. The inbreeding risk involved is probably just a little greater for them than for the breeder of purebreds on account of the slightly greater heterozygosis of the grades. Even if a breeder of grades is successful at linebreeding, he cannot sell at a premium the increased prepotency and uniformity

which would thus be put into his animals. He does not have the chance to gain as much by successful linebreeding as breeders of purebreds do. However, it sometimes happens that the breeder of grades uses a sire whose offspring turn out to be so much better than their dams that the inbreeding risk of using the sire on his own granddaughters or even on his own daughters seems worth taking. It seems likely that there are more breeders of grades who lose by failing to conserve a good sire than there are who lose by getting too many of the usual bad results of inbreeding while trying to linebreed to a good sire. For the breeders of grades, the certain merit of the animal to which he might linebreed needs to be further above the probable merit of the next sire which he would otherwise use than is the case with the breeder of purebreds.

Linebreeding is especially needed where there is much epistasis. Wherever a desired characteristic depends on a combination of genes which individually have undesired effects, those gene combinations tend to be scattered at each segregation. If inbreeding has made the family homozygous for several of these genes, the whole combination has more chance of being transmitted to enough of the offspring to permit its becoming established in that family. If the form of inbreeding used is linebreeding, with selection constantly directed toward keeping the family closely related to animals which once showed that desirable combination, the chances of recovering the whole combination among the descendants are much better than if the descendants were continually outbred to unrelated animals. Outbreeding would increase the likelihood that this particular combination of genes would be scattered into its constituent and individually useless parts. Linebreeding is the only very promising way of securing desirable gene combinations differing from the most frequent type of the breed by much more than four or five gene substitutions, each of which is harmful if made one at a time but beneficial if all can be made at once. That is, linebreeding is the answer to the situation pictured in Figures 20 and 21, in chapter 12, where it was pointed out that selection could carry a population to the nearest peak of desirability but could not carry it to a peak of higher desirability across an intervening valley which was more than a few gene substitutions in width.

DANGERS OF LINEBREEDING

The breeder may have the wrong ideal and be breeding toward a type which has a lower sale value than some other type. Of course this same danger exists in all other breeding systems. But, since linebreeding is more effective in carrying the breeder toward his goal, it is more important for a breeder practicing linebreeding to be sure of his goal

than for one who is breeding by individuality alone.

Linebreeding may be so intense that genes will become homozygous more rapidly than the breeder can discard the undesired homozygotes. The inbreeding may thus result in fixing in his herd some undesired genes in spite of all the selecting he can do against them. Whether this will happen depends not only on the inbreeding intensity but on the merit of the stock with which he starts and on the skill which he exercises in his selection, including such use as he makes of progeny tests, pedigree estimates, etc. Then, too, a part of the success or failure will be due to the chance inherent in Mendelian inheritance whereby one individual from a particular mating may happen to be a better or worse individual than would ever be produced again from that same mating.

There is no magic about the linebreeding process which will automatically produce good results. If selection is not practiced, a breeder will generally do better to avoid linebreeding altogether, since he would thereby avoid the inbreeding effect. But a breeder starting with good stock and directing the linebreeding toward the best of the recent ancestors in his herd can effect more improvement by selection while holding the improvement he already has than would be possible if he were continually outbreeding.

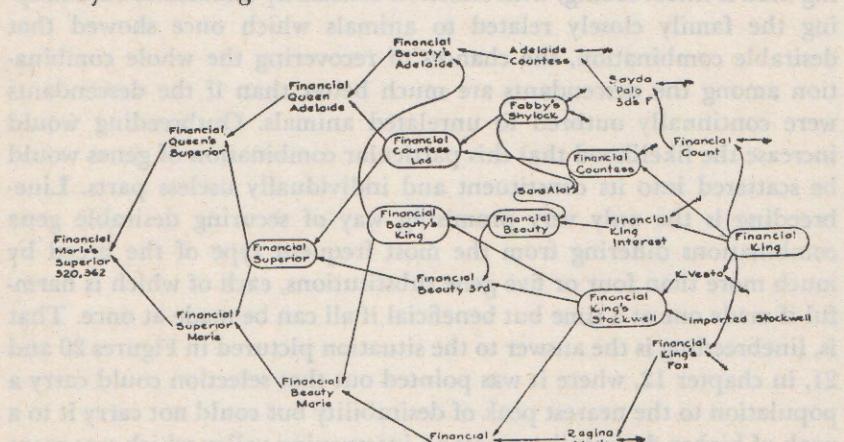


FIG. 40. Long-continued linebreeding within the Financial King family of Jerseys. Much of the linebreeding here is secondary and to recent animals such as Financial Superior, Financial Countess Lad, and Financial Beauty's King.

If one wishes to linebreed purely to one animal, he must see to it early that a large number of sons and daughters of that animal are saved. Otherwise the time quickly comes when further linebreeding to that ancestor also involves considerable linebreeding to some of its descendants. Figures 38, 40, and 41 show cases of that. There is no particu-

lar reason why this secondary linebreeding should be avoided if the animal toward which it is directed is an unusually good one. But, if the herd is small and only one man is linebreeding to this line, there will be only a few individuals in each generation. In some generations it will happen that no one of those will be outstanding enough to justify linebreeding to it. If the number of animals in this linebred strain or family

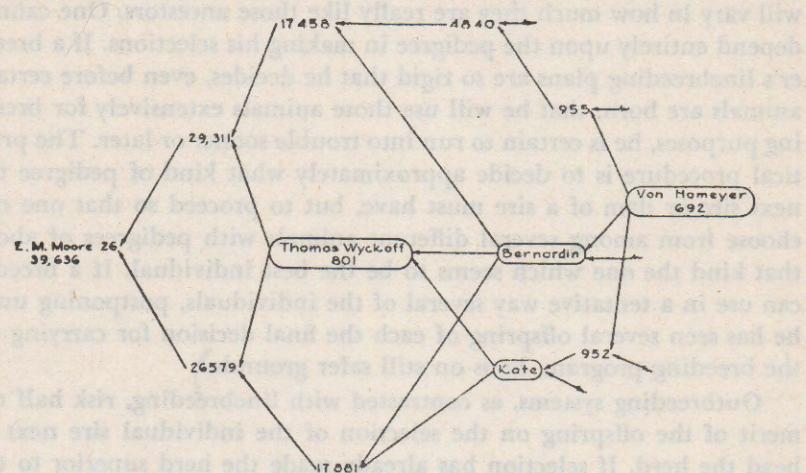


FIG. 41. A Rambouillet pedigree in which one male is the center of the linebreeding in each generation.

is very small, the breeder must either linebreed to some of those which were not good enough to justify it, or else he will have to give up his linebreeding plan and make a distinct outcross. This is the intrinsic danger of a permanent linebreeding policy based on too small a herd. If the herd is large enough, such secondary linebreeding can be avoided or at least can be kept so small in amount in those generations when there is no outstanding individual that it will be practically harmless. Hence, a linebreeding plan which is to last more than two or three generations without much risk requires the equivalent of a herd large enough to justify keeping about three to five sires in use at all times.² This might be one large herd; or several breeders with small herds might co-operate in breeding toward the same line, exchanging breeding stock with each other but rarely if ever introducing a breeding animal from herds not in the group.

GENETIC ASPECTS OF LINEBREEDING

(Linebreeding, more than any other breeding system, combines selection with inbreeding. In a certain sense, linebreeding is selection among

² These figures are based on the $1/8M$ formula for loss of heterozygosity within a closed group. (See Chap. 21.)

the ancestors rather than among living animals. Since many of the ancestors being considered will have had several different offspring, they are to some extent proved sires and proved dams. The linebreeding is, therefore, selecting from among progeny-tested ancestors those whose influence is to be preserved. This advantage is partly offset by the fact that the individuals used to preserve the traits of their ancestors will vary in how much they are really like those ancestors. One cannot depend entirely upon the pedigree in making his selections. If a breeder's linebreeding plans are so rigid that he decides, even before certain animals are born, that he will use those animals extensively for breeding purposes, he is certain to run into trouble sooner or later. The practical procedure is to decide approximately what kind of pedigree the next sire or dam of a sire must have, but to proceed so that one can choose from among several different animals with pedigrees of about that kind the one which seems to be the best individual. If a breeder can use in a tentative way several of the individuals, postponing until he has seen several offspring of each the final decision for carrying on the breeding program, he is on still safer grounds.

Outbreeding systems, as contrasted with linebreeding, risk half the merit of the offspring on the selection of the individual sire next to head the herd. If selection has already made the herd superior to the average of the breed, probably half of that will be lost in the next generation unless selection is again as effective as it was before. Every breeder will occasionally make mistakes in his selections. The breeder who continually practices outbreeding can therefore expect to have the merit of his herd at times go far back toward the average of the breed. One who wants to make and keep his herd far different from the average of the breed to which it belongs must put some kind of a pedigree barrier between it and the rest of the breed, so that the differences continually being produced as successive sires are used will tend to accumulate and not be halved with each successive sire. An analogy may make that point clear. Water tends to seek its level. If there were no barriers in the way, the level of the water in all the lakes of the world would quickly seek the level of the ocean, just as the water in the rivers is continually doing. The breeder who practices outbreeding is placing no barriers, except his own skill at selecting, in the way of his herd's tending toward the average level of the breed. The breeder who practices linebreeding is to a considerable extent isolating his herd from the rest of the breed, and its merit tends toward that of the isolated group rather than toward that of the breed as a whole, just as the level of the water in Lake Erie remains nearly constant but several hundred feet above the level of the water in the ocean, even though water is steadily flowing into it and out of it again.

SUMMARY

Linebreeding is a form of inbreeding directed toward keeping the offspring closely related to a highly admired ancestor. All inbreeding not necessary for holding this relationship high is avoided as far as possible. Hence, the intensity of the inbreeding is usually moderate in linebreeding systems. Relationship to a chosen ancestor is the main feature which distinguishes linebreeding from other forms of inbreeding.

Line breeding It is practiced to conserve the good traits of an outstanding sire or dam among its descendants, increasing those descendants in numbers without lessening their resemblance to this ancestor.

The more superior a breeder's herd or flock is to the average merit of its breed the more reason he has to practice linebreeding to his very best animals or to the very best of their recent ancestors.

The risk involved in linebreeding depends upon how much undesirable inheritance is in the herd when the linebreeding begins, upon how skillful the breeder can be in his selections, how much use he can make of progeny tests before he has to decide whether to use a sire extensively, how large his herd is, and whether he must work alone. If he can co-operate with several other breeders who are linebreeding to closely related animals, he can get an occasional mild outcross from them without disturbing his whole program.

Linebreeding is choosing which ancestors shall have their influence conserved and spread through the whole herd and which ancestors shall be allowed to diminish in importance with each generation until they no longer have much effect.

CHAPTER 24

The Family Structure of Populations

Even in populations which are breeding entirely at random, an individual does not have the same probability of being like every other individual. Each is more closely related to some than to others. This gives the population some kind of a family structure. Biological populations are not as homogeneous as a population of balls or numbered tickets in an urn, such as are often used to illustrate the elementary laws of probability.

The definition of family always has in it something of the idea that members of the same family are like each other and different from members of other families. Yet usage varies widely as to the degree of relationship which is meant. Sometimes family means a set of full sibs. This is frequent in poultry breeding, but so restricted a definition is uncommon in other animals where the number of full sibs is usually too small for this to be very useful. In plants which can be self-fertilized, family often means all the progeny of a single plant. It may mean a more highly inbred group than that, but usually "line" is then used rather than family. In animals which have long been linebred to a certain individual, family may mean the whole group of individuals which are linebred enough to be closely related to this individual and to each other. An example is the Owl-Interest family of Jerseys.

In animals where little or no linebreeding has been practiced, family is more likely to mean the descendants of a particular individual, usually a purchased one (a "foundation" animal) or one thought to be unusually good and with offspring well above average. Sometimes this usage is carried to extremes, the family name being traced back only through the female line (Shorthorns and Aberdeen-Angus) or only through the male line (Herefords) to an ancestor so remote that, if there has been no subsequent linebreeding, most of its descendants are little if any more related to each other than they are to other animals of that breed. Such usage is much like the transmission of family names in man. There is little more reason to expect any real average difference between Blackbirds and Ericas in Aberdeen-Angus than there is to expect differences between the Smiths and the Wilsons in the United

States or between the Hansens and the Larsens in Denmark! The idea of relationship between members of the same family becomes very dim here, and family names tend to become artificial designations which may be convenient but do not correspond to any biological reality.

Taxonomists use family in a special and definite sense to denote a group which is intermediate between a genus and an order, as the cat family (*Felidae*), the deer family (*Cervidae*), cattle family (*Bovidae*), etc.

We will consider first some of the less definite usages of family and then the family as a basis for selection.

THE FAMILY—A GROUP OF CLOSE RELATIVES

When we say that an individual is from a good family, we usually mean that the average merit of all its near relatives, regardless of whether they are related through the sire or dam or bear the same family name, is considerably above the breed average. This is the same sense in which the term is often used in man when someone is said to be of "a good family" or from "a shiftless family." Family, in this sense of the word, usually does not extend much farther among the collateral relatives than to first cousins. Not often is anything implied about ancestors farther back than the great grandparents, or about descendants much more distant than grandsons and granddaughters. This use of family is a practical application of relationship in estimating the heredity of an individual from the appearance and performance of a considerable number of its close relatives.

The family in this sense is somewhat indefinite, and one family grades into another. For example, an individual's maternal uncles and its paternal uncles are members of its family but the paternal uncles need not belong to the family of the maternal uncles at all. In fact, no two individuals would belong to exactly the same family unless they were full sibs. The individual is at the center of its family with its relatives clustered around it at various distances according to their relationship. There is no accurate and simple formula for giving proper weight to different relatives when averaging their good and bad qualities to find the merit of the family, although of course the closest relatives are the most important—unless there are strong environmental correlations between them, as may sometimes be the case with maternal sibs. If the family contains only a few members, chance can still play a large part in giving one such family a good rating and another one a poor rating.

THE FAMILY NAME

An Aberdeen-Angus cow is called an Erica if she traces through an unbroken female line to the cow called Erica, regarded as the foundress

of the family. Technically she is still an Erica even if she does not trace to Erica through any other line of her pedigree. In the Shorthorn and Aberdeen-Angus breeds the family name is traced through the dams. In the Hereford breed the family name is from the sire. In most dairy breeds the family name comes from the dam, but in some both systems prevail. The Holstein-Friesians have the De Kol family and the Pietertje family which take their names from foundation cows, but the Netherland family takes its name from the bull. In the Jersey breed such families as Tormentor and Golden Lad are named after bulls; but there are also such families as Coomassie, Fontaine, and Oxford named after cows. Breeders of cattle and horses mention family more than do breeders of sheep and swine.

This idea of family is a natural development in one-sire herds. A breeder with several cows but only one bull will, of course, observe many differences between his calves. Since all his calves in any one calf crop are sired by one bull, it would be natural to assume, without even realizing that he had done so, that all the differences between the calves were due to differences in their dams. If when the successive calves from the same cows are compared it is seen that there is a general tendency for one cow to have good calves and another one to have mediocre calves, it is natural for the breeder to group his animals in his own mind in terms of their dams or grandams, as far back as he remembers those. The inference that all the differences between the calves are due to differences in their dams is, of course, unjustified, since the sire is never entirely homozygous and some of the differences between the calves will be due to difference in the inheritance they have received from him.

This tendency for the owners of small herds to think of families in terms of female foundation animals is reversed in large herds where several sires are maintained at all times. It is difficult for the breeder to know all of his individuals closely in such herds and easy for him to compare the calves by one sire with their contemporaries by other sires. This naturally leads to a system of referring to the calves in terms of their sires and grandsires instead of their dams. Perhaps this is responsible for the fact that the Hereford breed, which is prevailingly bred in large herds, tends to trace its family through the male line, whereas breeds more commonly bred in small herds tend to trace the family through the dam.

When the system of tracing the family name through the dam is followed far, it naturally leads to printing the pedigrees in the "abbreviated" form, a sample of which is shown herewith in the pedigree of the noted Shorthorn bull, Rodney. Pedigrees in cattle breeds other than the Shorthorn are now usually printed in the bracketed form which

gives information on all lines to the same number of generations. Breeders of horses often use the abbreviated pedigrees. Formerly only that part of the pedigree which appears in columns in this example was shown. In recent years footnotes about the three most recent sires are added, as in this case. Figure 42 shows the pedigree as it would appear in bracketed form. The line drawn across the pedigree separates the information which is contained in the footnotes from that which is given in the columns.

RODNEY—753,273

Red. Calved February 8, 1917. Bred by C. H. Jolliffe, Darlington, Eng.

<i>Dam</i>	<i>Breeder of dam</i>	<i>Sire</i>	<i>Breeder of sire</i>
		Sanquhar Dreadnaught.....	A. M. & O. J. Law
Rosetta 7th.....	C. J. Jolliffe	Prince of the Blood.....	W. Duthie
Ballechin Rosetta.....	A. Robertson	Victor Chief.....	J. Durno
Scottish Rosebud.....	W. Duthie	Scottish Archer.....	A. Cruickshank
Red Rosebud 1st.....	S. Campbell	Gravesend	A. Cruickshank
Red Rosebud.....	S. Campbell	Borough Member.....	J. Bowman
Rosebud.....	S. Campbell	Novelist.....	S. Campbell
Rosebud 1st.....	S. Campbell	Diphthong.....	A. Cruickshank
Rosebud.....	S. Campbell	Scarlet Velvet.....	A. Cruickshank
Thalia.....	A. Longmore	Earl of Aberdeen.....	Mr. Hay
Myrtle.....	A. Longmore	Balmoral.....	A. Longmore

SANQUHAR DREADNAUGHT 680399, Sire, Hawthorn Champion 530142 by Bapton Champion (78285), out of Hawthorn Blossom 10th V46-585E. Dam, Zoe 11th V53-916E by Scotch Thistle (73584), out of Zoe 3d V44-502E.

PRINCE OF THE BLOOD 715108, Sire, Pride of Avon 311139 by Primrose Pride 222709, out of Rose Blossom V45-489E. Dam, Scottish Princess V52-677E by Scottish Archer (59893), out of Princess Royal 41st V46-455E.

VICTOR CHIEF 206990, Sire, Lord Lynedoch 206982 by Sittyton Pride 136401, out of Lenora V46-450E. Dam, Violet Blossom V44-406E by Lord Douglas 132003, out of Chief Blossom, V42-374E.

This abbreviated form of pedigree was fairly adequate when all of the breeders were acquainted with the sires which were being used in the prominent herds. There was no need to print the pedigree of the sire, since each potential customer knew that. The customer would not know all the females of the breed, so he did want to see the pedigrees of the cows. When the breeds grew larger the time came when no one knew all the sires; therefore, it became necessary to add these footnotes. The abbreviated pedigrees emphasize remote ancestors beyond all usefulness. For example, Rodney is called a member of the "Rosebud family" after the cow, Rosebud (by Scarlet Velvet), which was the first one bred by S. Campbell, who developed this family. If there has been no linebreeding to Rosebud in Rodney's pedigree, his relationship to her will be $(\frac{1}{2})^8$, which is about 0.4 per cent of his genes which probably came from her. Rodney must have had literally tens of thousands of contemporary relatives which had other family names but were more

closely related to him than was the cow from which his family name comes.

The abbreviated pedigrees emphasize the names of the breeders. The value of any pedigree is affected by the general reputation of the herd in which the animal was bred. Something worth while is lost when the name of the breeder is given a less prominent place than it has in

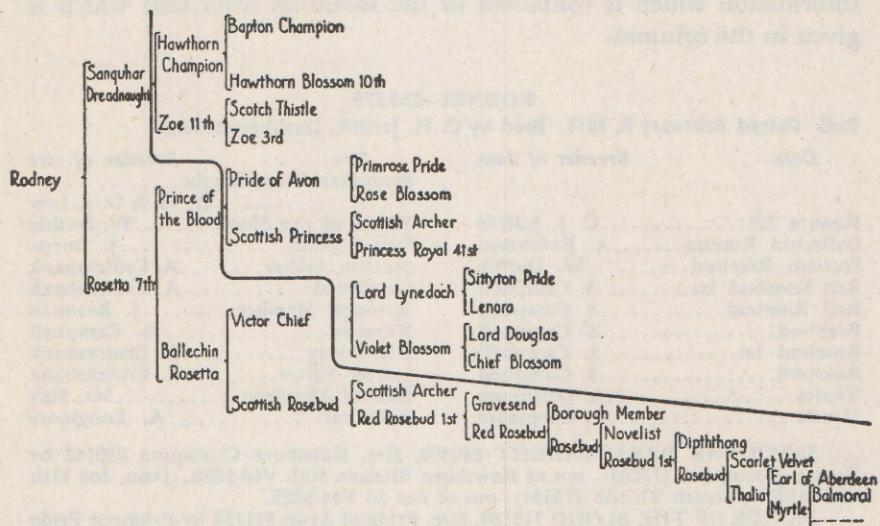


FIG. 42. The abbreviated pedigree of the Shorthorn bull Rodney, as it would appear if the same information, except the breeders' names, were given in the bracketed form.

the abbreviated pedigrees. Then, too, a cow does not get to be regarded as the foundress of a family on her own merits alone, but rather on the high merit of many of her offspring. It is fairly safe to infer that Rosebud 1st and also Rosebud (by Novelist) were distinctly better individuals than average or else Rosebud (by Scarlet Velvet) would not have been regarded as the foundress of a family.

The commercial importance of the family name is usually small, unless perhaps in times of booms or pedigree speculation. It lends itself well to speculation, particularly in breeds where the family name is traced only through the female line. Even the best of cattle are none too prolific, and a family can become famous and remain famous for many years without a large number of females of that family ever existing at any one time. If a strong demand for a family name can be created, extreme speculation can easily result because the supply is limited. Naturally such speculation is rare except when there is general prosperity and prices for breeding stock have been rising for some time. The

most noted case of this kind was the speculation that went on in the "pure" Duchess Shorthorns in the 1870's. There have been several periods of less extreme speculation in Aberdeen-Angus family names. Yet in 21 Aberdeen-Angus sales, studied from this point of view from 1929 to 1938 in Iowa (unpublished), the only conclusion possible is that practically no cash was really being paid for family name. However, this was in a period of economic depression and perhaps this finding is not significant. Four more sales from 1940 to 1942 when prices were rising showed distinct price differences between families.

The family name has genetic importance when the animal which gave its name to the family is still within three or four generations of the animals concerned. In such a case the coefficient of relationship between the animal and the foundation animal is still high enough to mean that the two are apt to be alike in a noticeable proportion of their genes.

Paying attention to maternal family names compels a certain amount of added attention to the females in breeding selections. Some breeders might be more careless about the dams if it were not for this extra attention forced on them by the family system. The actual importance of this may be slight.

The family name would have some genetic importance whenever the general condition exists that breeders strive always to mate a cow of one family to a bull of the same family; that is, to breed the family "pure." If S. Campbell had always sought Rosebud bulls to mate to his Rosebud cows, and if this had been continued to Rodney's time, Rodney would have been kept very closely related (linebred) to the original Rosebud cow. If that were a general practice among most breeders, it would lead to steady linebreeding which might keep the foundation animal important for many generations after its death. Where the family system brings this about, it can be a powerful instrument in improving the pure breeds, but this does not happen often. The cows in a small herd may belong to a dozen families, but the same bull is usually mated to all of them.

THE LINEBRED FAMILY

Sometimes "family" is used to designate a group which has been partially separated from the rest of the breed for a long time in their breeding and among which there has been considerable linebreeding. Not often have such cases really been carried far enough to make the family very distinct from the rest of the breed. Even a slight separation of this kind has sometimes been the occasion for a large amount of speculation in pedigrees. The most famous case is that of the "pure" Duchess Shorthorns, for which the pedigree speculation reached its

climax in 1876 in the New York Mills sale where one cow sold for \$40,600. The "pure Scotch" Shorthorns are another example. In spite of many bitter condemnations of the "straight Scotch" craze, the straight Scotch almost entirely displaced the other beef Shorthorns in the United States during the two decades preceding 1920. The "straightbred" or "airtight" Anxiety 4th Herefords may be a similar case in which the final outcome is still in doubt. These straightbreds are a group whose pedigrees in nearly every line go to daughters of North Pole and to sons and daughters of Anxiety 4th. That is, they carry nearly 50 per cent of the blood of North Pole and Anxiety 4th combined. Somewhat milder cases have happened in the Jersey breed in connection with the Owl-Interests, the St. Lamberts, and Tormentors, and in the Holstein-Friesians with the Homestead family.

The principles involved are just the same as those that have been discussed under linebreeding. If the linebreeding has been carried far enough to make the family really distinct from the rest of the breed, then there is an important genetic basis for the family name. This kind of a family is to some extent a breed within a breed.

THE GENETIC DEFINITION OF FAMILY

The biological basis for treating a group as a family is the average genetic likeness among members of the group. The best estimate of genetic likeness where the actual genotypes are unknown is the coefficient of relationship. This will usually give a reasonably true picture of the average genetic likeness of family members where the base to which relationship was computed is not many generations in the past.

As an example of this way of defining a family quantitatively, we might choose to consider each set of full sibs in a random breeding population as a family. For comparison with other kinds of families we can define this kind as a group which are related to each other 50 per cent. If all the offspring of each male are to be considered as a family, that kind of a family can be defined as a group related 25 per cent to each other.¹ We can compare the importance we should attach to family when making selections in the two cases by using alternately .50 and .25 for r in the formulas which are in the next few pages. If all the grandsons and granddaughters of a male are to be considered as a fam-

¹ Although such a family will not be entirely homogeneous if some of them are full sibs to each other, this will not increase the average relationship much if there are more than three or four different sets of such full sibs or if the number in each such set is small. For example, if the progeny of a boar consist of four litters of five pigs each and we call this a family, it will not of course be a perfectly homogeneous family but will be one large family with four branches or subfamilies. The average relationship of each pig to the other 19 will be an average of 4 full sib and 15 half sib relationships or about 30 per cent. If the progeny of a bull are five pairs of full sisters, the average relationship within the group of 10 will be an average of 1 full sib and 8 half sib relationships or 28 per cent.

ily, we can define this family as a group which are related to each other 6½ per cent, plus a little more from the fact that some of them will be sibs or cousins through more than one grandparent. When family is thus defined quantitatively, it is easy to see why the practical usefulness of family groupings becomes so small when the group members are related only through ancestors as distant as grandparents.

The observed family resemblance may be expressed either in terms of the correlation between members of the same family or in terms of how much smaller the differences between members of the same family are than the differences between members of different families. The formula which relates the two is simply that the correlation between

members of the same family equals $\frac{V - B}{V}$ where V is the variance between individuals which belong to different families and B is the variance between individuals which belong to the same family. $V - B$ is the variance caused by things which are alike for all members of each family but may vary from one family to another. $V - B$ might be wholly genetic in some cases but is likely also to include some differences caused by common environment for family mates, or by epistasis, or dominance.

The formulas showing quantitatively the advantages and disadvantages of selection on a family basis are rather complex but they are given in the following sections because they are important guides for estimating whether a plan for selecting on a family basis is likely to increase progress sufficiently to be worth its costs.

CONDITIONS AFFECTING PROGRESS WHEN CHOOSING BETWEEN FAMILIES

The formulas for comparing individual and family selection, when the same percentage of the population must be culled in either case, are expressed as follows for convenience:

Let G = the additively genetic variance between individuals.

E = all other variance (largely environmental in most cases)
which is random with respect to family.

C = the variance caused by whatever fraction of the environmental, epistatic, and dominance deviations are alike for members of the same family, but vary from one family to another.

r = genetic relationship between members of the same family.

t = phenotypic or observed correlation between members of
same family = $\frac{rG + C}{G + C + E}$.

n = number of individuals in each family.

Then: Variance between individuals from different families =
 $E + G + C$

Variance between members of the same family = $E + (1 - r) G$.

Variance between actual family averages =

$$rG + C + \frac{(1-r)G}{n} + \frac{E}{n}.$$

Having large numbers in the family permits the environmental differences (E) and the genetic differences between members of the same family—the $1-r$ fraction of G —to cancel each other, so that the actually observed differences between family averages tend toward $rG + C$, which will be almost wholly genetic if C is very small. When n is small a considerable part of the differences between the actually observed averages of various families may still be due to the E/n term which is environmental and misleading.

The larger r is, the more of the genetic variance (G) will be between families instead of within families. This will permit the family averages to be farther apart, so that one can reach farther when selecting between families when r is large than when it is small. Also any increases in r will make a larger fraction of the observed differences between family averages genetic, so that one selecting between family averages will actually get a larger fraction of what he reaches for. To have r large is an important prerequisite for selection between families to be very useful.

When C is large the heritability of differences between family averages will be low, since that heritability tends toward $\frac{rG}{rG + C}$ as n becomes indefinitely large. Hence, with C large many of the differences between family averages will not be genetic, many mistakes will be made in selecting between families, and only a small fraction of what is reached for in family selection will actually be gained in the merit of the offspring. The deceiving effects of C do not diminish with increases in n as those of E do. In the mammals, C is especially likely to be important when the family consists of maternal sibs.² C is likely to be large also in birds which hatch and brood their own young. Even in birds hatched in incubators and reared apart from their dams, certain initial environmental differences caused by the size of the egg may not be wholly equalized before the birds are adult. In data collected from

² Environmental correlations between full sibs are also prominent in data on man, especially in data pertaining to mental and social traits. Man's long infancy and childhood and the wide differences from home to home in cultural environments and parental precepts and examples give an unusual opportunity for such correlations to develop in characteristics which are susceptible to much modification by such influences.

many different farms, C is often Troublesomely large because environments vary considerably from farm to farm, and in most cases each family will have been raised wholly on one farm. In carefully planned breeding experiments every effort will be made to reduce C to zero by controlling or randomizing the environment with respect to families. Often that can be fairly well achieved for all of C except the part due to maternal environment and the part due to weather and to changes in general environment from year to year in cases where the families are not contemporary. But breeders when purchasing animals usually must compare families kept in different herds. Then the best they can do to eliminate C is to observe the conditions under which each family is kept and make allowances for the differences which they think these conditions produced between families.

FAMILY SELECTION COMPARED WITH INDIVIDUAL SELECTION

For clarity we will first consider what family selection would accomplish if it were practiced by itself without any attention to individuality. Figure 43 will illustrate the difference between family selection alone and selection on an individual basis. The data are 180-day weights of four pigs in each of four litters. One-fourth are to be saved for breeding purposes, and selection is for the heaviest weights. If selection is wholly on a family (litter) basis, the selected pigs will be all four of those in family 2, since that family has the highest average weight. Pig E , which has a low weight, will be selected along with the other three because it is in the family with the high average. If selection is wholly on an individual basis, pigs D , G , H , and L , will be selected regardless of the merits of their sibs. If the method of selection is some compromise which gives attention to family averages as well as to individual merit, pigs F and P might possibly be saved instead of pigs D and L .

Two things about this situation must be emphasized. First, one cannot pay attention both to family and to individuality without compromising on both. Almost never will it happen that *all* members of the family which has the highest average will be individually superior to *all* members of the other families. One must compromise on one thing or the other when deciding what to do with good individuals (like D and L) from mediocre or poor families and with mediocre or poor individuals (like F and E) from a good family. Second, some of the same animals will be saved, no matter which method or compromise is used. The family with the highest average *must* contain more than a fair share of individuals which are above average. G and H illustrate this. Purely individual selection does some of the same things which purely family selection would do. If either method is *absolutely* ineffective, the other

will be also. The contrast between them is between two methods both of which will produce some improvement, if either of them will produce any, but which will not, except by coincidence, produce exactly the same amount of improvement per generation.

LITTER NUMBER	INDIVIDUAL PIGS				LITTER AV.									
1	A	B	C	D	183									
2	E		F	G	H	199								
3	I	J	K		L	150								
4	M	N	O	P		188								
	110	120	130	140	150	160	170	180	190	200	210	220	230	WEIGHT AT 180 DAYS (Pounds)

FIG. 43. Distribution of some pig weights by litters to illustrate family and individual selection. Each pig is designated by a letter located vertically according to its litter and horizontally according to the pig's weight.

The increase in the population mean each generation under purely family selection is expected to be the following fraction of the increase

to be expected under purely individual selection: $\frac{1 + (n - 1)r}{\sqrt{n[1 + (n - 1)r]}}$.

Although this formula is complex, it can be seen that family selection is most likely to be superior when r is large and t is small. Differences in n do not affect the ratio very much unless t is extremely small and r is large. In that case high values of n increase the effectiveness of family selection markedly. If t is nearly equal to r , family selection cannot equal individual selection in effectiveness, even when r and n are large.

If purely family selection is to produce improvement x times as rapid as would be produced by individual selection, then r must equal

$\frac{x\sqrt{n[1 + (n - 1)r]} - 1}{n - 1}$. For x to be 1.0 when families consist of 5, r

would have to be:

.41 if t is .1	
.50 " " .2	
.58 " " .3	
.65 " " .4	
etc.	

If n is as large as 25, the corresponding values of r necessary for x to be 1.0 would be only a little lower, namely: .34, .46, .56, .64, etc. In short, if family selection is to be much more effective than individual selection, r must be considerably larger than t . Increases in n do not lower the requirements for r much unless t is very small.

Because t equals $\frac{rG + C}{G + C + E}$, it is necessary for C to be nearly

zero and E to be much larger than G if r is to be much larger than t . When heritability is low (G is small, compared with $E + C$) neither individual selection nor family selection will make rapid progress, but family selection can then be considerably more effective than individual selection if C is zero or nearly so. Among important characteristics for which E is likely to be very large and C may be small, are such complex things as fertility, vitality, longevity, disease resistance in general,³ and probably growth rate so far as that does not depend mainly on dimensions of bones.

SUPPLEMENTING INDIVIDUAL SELECTION WITH FAMILY SELECTION

It is sensible of course to use both the family average and the individual's own characteristics in selecting, compromising somewhat on each in order to make faster progress than could be made by using either alone. The progress per generation which will be achieved under the optimum combination of individual and family selection will be the following fraction of what would be achieved by selection on individuality alone:

$$\sqrt{1 + \frac{(n - 1)(r - t)^2}{(1 - t)[1 + (n - 1)t]}}$$

The most important thing in determining how large this ratio will be is the term, $r - t$, which measures how much more the members of the same family are like each other genetically than they are outwardly. When $t = r$, nothing at all is gained by paying attention to the family average. The larger the difference between r and t the more there is to gain by paying some attention to family. Even when t exceeds r , something is to be gained from considering the family average, but in this

³ Individual differences in resistance to some specific diseases may be rather highly genetic.

case the attention given to the family average is negative; i.e., the individual is judged partly by its own merit and partly by how much it deviates from its family average, instead of being given some credit if the average merit of its family is high and being penalized if it is from a poor family.

The numerical values in Table 18 for some selected conditions may make it easier to see what circumstances lead to much gain from paying attention to family. The basic formula is that if paying attention both to the individual and also to its family average is to make progress $1+y$ times as rapid as if selection were on individuality alone, $r-t$ must equal

$$\frac{y(2+y)(1-t)[1+(n-1)t]}{n-1}$$

For progress to be made 20 per cent faster by considering the family average requires the difference between r and t to be 1.45 times as large as is necessary to increase progress by 10 per cent. If progress is to be 30 per cent faster, the difference between r and t will need to be 1.81 times as large; for 40 per cent it will need to be 2.14 times; for 50 per cent 2.23 times is required; etc.

Since r cannot exceed 1.0, extremely large gains from paying atten-

TABLE 18
GENETIC RELATIONSHIPS NECESSARY IF PAYING ATTENTION ALSO TO FAMILY IS TO
INCREASE THE RATE OF IMPROVEMENT BY 10 PER CENT OR BY 100 PER CENT

t	For Progress to Be 10 per Cent Faster ($y = .1$)		For Progress to Be Twice as Fast ($y = 1.0$)	
	When $n = 5$ r must =	When $n = 25$ r must =	When $n = 5$ r must =	When $n = 25$ r must =
.01	.27	.11	.89	.40
.05	.29	.19	.97	.56
.10	.36	.26	Impossible	.72
.20	.47	.40	"	.96
.30	.58	.52	"	Impossible
.40	.69	.64	"	"
.50	.78	.74	"	"
.60	.87	.83	"	"

tion to the family average are possible only when t is very small. Also n must be large, but this of itself will not help much unless t is so small that $(r-t)^2$ is far larger than $t(1-t)$. This marks out the domain in which family selection is most useful, for t can be small only when heritability is low and when other causes (C) for family members resem-

bling each other are zero or very nearly so. Then if r and n can both be made large, selection on the family basis can increase progress very much.

Family selection and individual selection are mainly supplementary procedures rather than competitive ones, individual selection doing nearly all that the two together could do when heritability is high but declining in effectiveness in direct proportion to the decline in heritability, while family selection helps little when heritability is high but increases in relative effectiveness as heritability of individual differences declines. Thus, in framing efficient breeding plans, attention should gradually shift from individual selection to emphasis on family selection more and more as one turns from highly hereditary to less and less hereditary characteristics.

OPTIMUM ATTENTION TO PAY TO FAMILY AVERAGE AND TO INDIVIDUAL MERIT

For the maximum rate of improvement, each bit of merit or defect in the family average should receive $\frac{n}{1 + (n - 1)t} \cdot \frac{r - t}{1 - r}$ times as

much attention as the same absolute amount of merit or defect in the individual's own characteristic. This ratio is large when r is large, t is small, and n is large, although the latter doesn't make much difference unless t is small. This ratio goes to zero when $r = t$ and takes negative values when t exceeds r . For t to exceed r means that C is large and that each family average is being shoved up or down by circumstances other than the average breeding value of that family. That the fraction then is negative merely indicates that it is then more accurate to judge the individual partly by its deviation from its family average, as an automatic way of correcting partly for the nongenetic circumstances included in C . The deviation of the individual from its family average is composed of variation coming from E and from $(1 - r)G$ and does not include the C term. To judge the animal entirely by its deviation from its family average would open the door to large errors from E and would forego opportunity to select for differences caused by rG . Hence the optimum combination of attention to family and to individuality is a compromise aimed at some discounting of C , some use of rG as well as $(1 - r)G$, and some reduction of E by n .

The conditions when attention to the family average should turn negative may actually be reached in data where r is low and C is large, as in dairy production records used in proving bulls which have been kept and used in different herds. Also characteristics markedly influenced by prenatal or pre-weaning differences in environment are likely

to have a large G between litter mates. For such characteristics in pigs, full sibs which are not litter mates or even paternal half sibs may deserve more attention than litter mates.

INBREEDING AND THE FAMILY STRUCTURE OF POPULATIONS

Inbreeding helps in several ways to make family selection more effective. First it increases G to $1 + F$ times what it was in the foundation population.⁴ This also helps mass selection by increasing the standard deviation a little and thus making a larger selection differential possible. A more important effect is that it increases heritability, and thereby a larger fraction of the selection differential is actually gained in the offspring. The gain had by increasing G is rather quickly exhausted when the poorer families are culled. To renew it the remaining families must be intercrossed and distinct families formed again by inbreeding these crosses. It is therefore a gain which cannot be harvested in every generation.

In the second place, inbreeding is the only way to make r much larger than .31 in large families of the less prolific animals, or larger than .50 in families of animals like pigs and chickens. As a numerical example of how rapidly inbreeding will increase r , the full sibs in the first inbred generation of full brother-sister inbreeding are related 60 per cent, in the second generation 74 per cent, and in the third generation 79 per cent—compared with 50 per cent where there is no inbreeding.

The r between full sibs equals $50 \left[1 + \frac{F + F'}{1 + F} \right]$ per cent, F

being the inbreeding of sibs and F' the inbreeding of their parents. This shows vividly for full sibs how closely the increase in r beyond 50 per cent depends on the intensity of inbreeding. In continuous half sib inbreeding—one sire in a large herd closed to outside blood—half sibs in the first inbred generation are related 39 per cent, in the second generation 50 per cent, and in the third generation 58 per cent. How rapidly inbreeding will increase the genetic relationship between half sibs may be seen from the fact that this relationship equals

$25 \left[1 + \frac{5F + F'}{1 + F} \right]$ per cent, provided the three parents are equally inbred and equally related to each other.

Even one or two generations of rather mild inbreeding can raise r enough to increase greatly the proper amount of attention to pay to the family average for the most effective selection, especially if the charac-

⁴ The increase will generally be somewhat more than this if there is much dominance or epistasis. But G may actually decline if enough of the poorest families are culled while the inbreeding is being done.

teristic is only slightly hereditary, since then the accompanying increase in t would be far less than the increase in r . This may be a very practical procedure under many circumstances, since the risk of inbreeding degeneration would not be large, it would take only a generation or two to produce this much inbreeding, and therefore a selection between families could be made every second or third generation. To carry inbreeding to higher levels before making the selections between families would make both r and G larger and would make selection between families more effective in the generation in which it was practiced, but would involve more inbreeding risk and would require more generations for each cycle of inbreeding, selection, and re-crossing the selected families. Therefore, it might make less net progress per generation than the shorter cycles with the milder inbreeding. Not all of these relations have been explored yet, but it appears⁵ that not much is to be gained by increasing the inbreeding much farther than 30 per cent before selecting between the lines, unless epistatic interactions are highly important.

A third way in which inbreeding can make family selection more effective is that it permits high values of r without necessarily having high values of G in those characteristics where maternal environmental influences are strong or where contemporaneity carries with it some strong environmental correlations. Without inbreeding it is difficult to get families which have r much larger than .31 and yet are not maternal sibs, and impossible to get such families with r as large as .38. Yet in the second inbred generation of continuous half-sib inbreeding, the members of the same family will already be related to each other 50 per cent and in the third generation 58 per cent, although they are not from the same dams.

The close relation between intensity of inbreeding and distinctness of families is shown by the speed with which, in a population inbred steadily without selection, the genetic variance tends to be shifted from variance within families, $(1 - r) G$, to variance between families, rG . In regular full-sib inbreeding, rG equals $(1 - r) G$ before the inbreeding begins, is 1.5 times as large in the first inbred generation, 2.7 times as large in the second, 3.8 times as large in the third, etc. In regular half-sib inbreeding the corresponding ratios are .33 before the inbreeding begins, .64 in the first inbred generation, 1.00 in the second, 1.40 in the third, 1.86 in the fourth, etc. The general formulas are that rG equals $2fG_0$ and $(1 - r) G = (1 + F - 2f) G_0$ where F is the inbreeding of the animals concerned, f is the average inbreeding of the offspring which

* Dickerson, G. E., 1942, Experimental design for testing inbred lines of swine, *Jour. of An. Sci.*, Vol. 1.

would be produced by mating members of the same family together, and G_0 is what G was in the foundation generation to which the inbreeding and relationship coefficients are traced. The ratio of the genetic variance between unrelated lines to that within lines thus

$$\text{becomes } \frac{2f}{1 + F - 2f}.$$

This forming of families between which selection could then be more highly effective may have been the major part which inbreeding played in the development of hybrid corn. The inbreeding was carried so far that r was nearly 1.0 and G was nearly doubled. In that condition the differences between lines were almost wholly genetic (except for whatever there was in C), and selection between them for their combining power could be more effective than ever before. However, this is not the whole story, for the inbreeding also aided greatly in purging the lines of rare and undesirable recessives, and was almost the only means for isolating and comparing epistatic combinations. These effects may have been very important, too.

FAMILY DISTINCTNESS AS AFFECTED BY DOMINANCE AND EPISTASIS

In random breeding populations most of the effects of dominance are included in the E term, but when members of a family are related through both parents of each, there is some correlation between their dominance deviations. This contributes a little to the C term in such families. If a population is being inbred, the heterozygotes become scarcer and the variance caused by dominance deviations tends to disappear, part of it going to join the increases in the G term.⁶ Thus the general effect of dominance is to make the E term distinctly larger and the C term a little larger than if there were no dominance. It makes the effectiveness of family selection increase with advancing inbreeding a little more than the preceding formulas indicate.

Variance due to epistatic gene interactions likewise goes mostly into the E term when inbreeding is zero, but the epistatic deviations of family members are correlated, and this contributes something to the C term. As inbreeding gets more intense, the correlations between epistatic deviations of members of the same family rise with r at an ever-increasing rate. This increases C , but also some of what were epistatic deviations in a random-breeding population can be gathered into the additive scheme in partially inbred populations. This increases G at the expense of E and perhaps of C . The net result is that family differences

⁶This is curvilinear, and there are certain special but uncommon combinations of circumstances under which the variance due to dominance deviations would increase a bit in the early stages of inbreeding, before beginning to decline.

and distinctness become even more pronounced with increasing inbreeding than was indicated in the preceding formulas. Presumably this makes family selection more advantageous than the preceding formulas indicate.

RELATED FAMILIES

In actual populations the families are not wholly unrelated to each other. Instead each family is related to others—to a few closely, to some less closely, and to most scarcely at all unless the relationship is relative to a basis farther back than the time when this population first diverged from other populations. The family structure of a population is somewhat like a fishing net in which each knot is rather close to a few others but distant from most.

Since each individual has two parents but the number of its offspring can vary from zero to many, the network of descent as traced backward will necessarily be more regular than when traced forward. If there has been some degree of inbreeding and separation of the population into small and partially isolated subgroups between which there is little inbreeding, the irregularity of the family structure of the population may become extreme. It is somewhat like an irregularly torn and tangled net, some clumps of strands being heavily intertwined with each other but swinging almost free from adjacent strands and only remotely connected with the rest of the net. Some of the subgroups themselves at a later date may be subdivided still further into partially non-interbreeding groups. Thus arise families within families.

When selection is to be practiced between such related families, the effective r between members of the same family is approximately $\frac{r_2 - r_1}{1 - r_1}$ where r_2 is the relationship within the family, and r_1 is the relationship of the two families to each other. For example, suppose two families are related 20 per cent to each other, but the relationship within families is 50 per cent. Then, for selecting between two individuals each belonging to one of these families, the r in the preceding formulas for determining how much attention to pay to the family average is approximately $\frac{.5 - .2}{1 - .2}$, or about 38 per cent. The practical consequence is that when separate families are built from a common and closely related foundation stock, the inbreeding needs to be pushed further for selection between families to reach a given effectiveness than if each had been started from an unrelated stock. When selecting between individuals from related families, the family averages should receive less attention than when selecting between individuals from unrelated families. The common sense of this is obvious when one considers the extreme case of

selecting between full sibs. The family average is useless for helping discriminate between them, since it is exactly the same for both. In selecting between two half sibs the family averages of each are partly determined by the common parent. To that extent the family averages are less helpful in indicating which of the two has the higher breeding value. The discussion here and formula for effective r merely generalize the principle of this and extend it to less obvious cases.

SUMMARY

The term "family" in animal breeding implies a group of animals related to each other, but usage varies widely as to how close that relationship must be before two individuals are considered as members of the same family. Often the definition of family is vague and variable, even in a single discussion.

Family often signifies a name which is handed down, perhaps for many generations, usually through the female line but occasionally through the male line. As such it has no more real significance than human family names do. However, it lends itself to speculation in boom times and has sometimes played a part in making some purebred individuals sell for higher prices than others of the same breed. It may help emphasize the breeder's name. It may make selection of females a bit more strict than would otherwise be the case.

If females are consistently mated to males of the same family as their own, such linebreeding tends to make and keep families distinct from each other. If the linebreeding is continued long or becomes intense, such a linebred family tends to become a breed within a breed. Such distinct families within pure breeds have been formed only occasionally.

The family has a measurable genetic basis and practical usefulness when it is defined as a group with an average genetic relationship, r , to each other. Attention to family is most helpful when r is large and the observed resemblance of family members, t , is low. Each bit of merit or

defect in the family average should receive $\frac{r-t}{1-r} \cdot \frac{n}{1+(n-1)t}$

times as much attention as the same amount of merit or defect in the individual.

The family should be given negative attention when the observed resemblance between family members is higher than their genetic resemblance. This means that the individual should be judged partly on its own characteristics and partly on its deviation from its family average.

The family averages should receive less attention when comparing two individuals from related families than when comparing individuals from unrelated families.

Inbreeding is necessary for making families with r much above .31 in the less prolific animals or above .50 in any animals. If individual variations in the characteristic are only slightly hereditary, the increases which inbreeding makes in r will be much larger than the increases in phenotypic resemblance. Then the gain from paying attention to the family average in selection may become large.

If epistatic effects and dominance are important, increases in inbreeding will increase family distinctness and family differences even more than the formulas in this chapter indicate.

Characteristics which can take only a twofold classification in the individual animals and which are subject to considerable chance variation need very much the help of family selection, because the error in individual selection is high. Vitality, or disease resistance in general, are examples if the animal's success or failure can be measured only by whether it lived or died.

Family selection is most helpful for characteristics for which heritability is low and family members do not resemble each other for any other reason than their genetic relationship.

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CHAPTER 25

Blood-Lines

The word "blood-line" is often used by breeders and is found in many advertisements and current animal breeding writings. It is rare, however, in textbooks on animal breeding and still rarer in textbooks on genetics.

In general, blood-line is synonymous with pedigree but is not so definite. Sometimes it is used more nearly in one of the senses of family, as, for example, when a man suggests performance testing of many animals in a breed to find out "which blood-lines are the most productive and valuable," or wants to learn "which are the most prominent blood-lines of the breed."

Sometimes blood-line is used to convey the idea of relationship, as when a man says that two animals "have nearly the same blood-lines," or that some animal "has valuable blood-lines." In the first case he implies that the two animals are closely related, and in the second case he implies that this animal is closely related to some ancestors whose descendants are highly valued. As a measure of relationship blood-line is an indefinite and sometimes misleading substitute for the probability of likeness which is expressed accurately in the coefficient of relationship. Usually it makes the relationship seem much higher than it really is. Blood-line is a convenient term, however, because almost everyone understands it in a general way.

Sometimes blood-line is used to describe a linebreeding or an inbreeding program, as when a breeder says he "believes in mating together animals of similar but not identical blood-lines." He thus conveys a vague idea of what would be more precise but probably not so readily understood if he used the inbreeding coefficient and the relationship coefficient to state how intensely he planned to inbreed and how closely he was trying to keep his herd related to some noted ancestor.

Sometimes blood-line is used to infer that a whole complex of inheritance is transmitted as a unit unchanged from parent to offspring, generation after generation. This idea comes from studying pedigrees