

mals are unrelated in the nearest ten generations of their pedigrees, the thousand ancestors of the one cannot include any of the nearly contemporary thousand ancestors of the other. If there has been no inbreeding, each animal has more than a million ancestors in the twentieth generation of its pedigree. If the pedigree is followed much further, these numbers become greater than the number of animals alive at that time could have been. For example, in man there are about three generations to the century. The number of ancestors each person had living at the time of William the Conqueror would be about 2^{26} , or roughly a little more than 67 millions, if there had been no mating of relatives. Now there never were that many people in Great Britain at any one time. Anyone descended entirely from British ancestors must have had an enormous amount of repetition of ancestors that far back in his pedigree, especially since many individuals living at any one time leave no descendants. One whose ancestors came from several nations has only to follow his pedigree a few centuries further back (no further than to 900 A.D. at the outside) to find that, if there had been no mating of relatives, he would have had more ancestors alive at that time than there were people on earth!

This situation is more extreme in livestock breeding. The Brown Swiss breed in the United States is descended entirely from 129 cows and 21 bulls which were imported into this country. In American Rambouillet pedigrees about 45 per cent of the lines traced back at random end in sheep from the von Homeyer flock in Germany. Over half of the random pedigree lines of the Shorthorn breed go to one bull, Favourite. Similar things are true of other breeds, although few breeds are yet explored in detail from this point of view. Moreover, this includes only what has happened since pedigree recording began. That is a comparatively short time—about 150 years in the Shorthorns and only about 50 years in the other two breeds mentioned.

The definition of inbreeding *must* be relative to some group or population. Pure breeding, for instance, is inbreeding relative to the whole species but need not be and rarely is inbreeding of noticeable intensity relative to the breed. Figure 34 illustrates the situation diagrammatically from closest inbreeding to widest outbreeding. To the left of random mating are the inbreeding matings while the outbreeding ones are to the right. The closeness of the two lines to each other in Figure 34 represents how closely the mates are related to each other. That ranges from complete identity in the case of self-fertilization (possible in most plants but impossible in any farm animal) through close relatives, members of the same breed, members of different breeds but the same species, members of different species within the same genus,

and perhaps even members of different genera. The offspring of species crosses usually exhibit some degree of sterility. Generic crosses are very rare. Presumably the genotypes of the individuals are so unlike that the union, even if possible at all, produces no living offspring.

THE CONSEQUENCES OF INBREEDING

(The primary effect of inbreeding is to increase the probability that the offspring will inherit the same thing from sire and dam. This tends

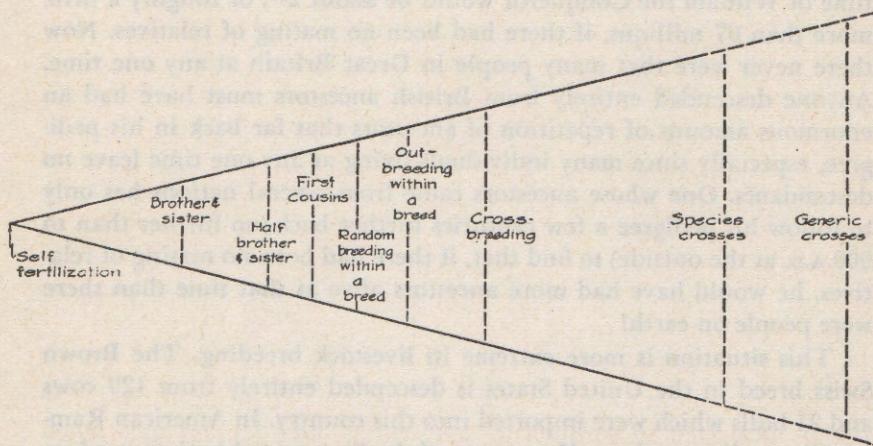


FIG. 34. Degrees of inbreeding arranged according to the relationship between mates.

to lower the percentage of heterozygosity in the population and to produce relationships higher than 50 per cent. All the other effects of inbreeding result from those. In each inbred line the genes which are to be in the next generation are a sample of those which were in the preceding generation. Because the sample is small the gene frequency in it will often by chance differ considerably from the gene frequency in the generation from which the sample came. Thus the gene frequency can wander back and forth until it reaches either zero or one. Then the line is homozygous for that particular gene or its allele. This homozygosity cannot be lost, except by mutation, as long as the inbreeding is continued. The genes which are heterozygous are still subject to the possibility of becoming homozygous each generation the inbreeding continues. The fewer animals there are in the inbred line the smaller is the sample of gametes which are needed to constitute the next generation and the farther the frequency of each gene can drift up or down in any one generation.)

Because this change in gene frequency is random (equally likely to be up or down), inbreeding is in conflict with selection whenever selec-

tion is tending to keep a gene at some equilibrium frequency, as when the heterozygote is preferred. Inbreeding is continually causing the gene frequency to drift away from that equilibrium point in either direction and selection is continually tending to take it back there. When the inbreeding is very mild and selection is intense, the gene frequency cannot get far from its equilibrium value. But when the inbreeding is intense it may overwhelm selection and carry gene frequencies far away from their equilibrium values, some above and some below.

If the inbreeding is intense and continues long enough, and if there are no mutations, the ultimate condition approached in each inbred line is complete homozygosis in all pairs of genes. In some pairs it will be the less desirable and in other pairs the more desirable gene which becomes homozygous. Each inbred line is likely to differ from every other inbred line in regard to which particular combination of genes becomes homozygous in it, if many different pairs of genes are involved. Inbreeding in animals almost never comes close to complete homozygosis in actual practice. Even self-fertilized plants reach an equilibrium point where the further loss of the remaining small amount of heterozygosity just equals the new heterozygosity which mutations produce in each generation. Mutations are so rare that for practical purposes they can be neglected in considering inbreeding but they are mentioned here for completeness.

The Mendelian basis of the inbreeding effect can be illustrated most simply by the extreme case of self-fertilization. Each generation in each inbred line consists of one individual in which, of course, each gene is either homozygous or heterozygous. That is, gene frequency can have only the values: .0, .5, or 1.0. Genes which are already homozygous in the whole line must remain so as long as the inbreeding continues, unless a mutation occurs. Pairs of genes which are heterozygous may be considered as a population of the two kinds of genes in equal numbers, from which two genes are to constitute the population in the next generation. The probabilities that those two will be *AA*, *Aa*, or *aa*, are in the ratio 1 : 2 : 1. Thus half of all heterozygous genes in a self-fertilized individual may be expected to become homozygous in its offspring. Selection favoring either homozygote will tend to hasten the rate of approach to homozygosis, while selection favoring the heterozygote will tend to retard it. If there are many heterozygous pairs of genes, several will become homozygous in every individual; and selection can have only trivial effects in delaying any such rapid rate of approach toward homozygosis. For example, if a self-fertilized individual is heterozygous for 10 pairs of genes, only 1 offspring in 1,024 would be as heterozygous

as its parent. Even in species with reproductive rates which would permit intense selection, it would be impossible to recognize genotypes accurately enough to find such a rare heterozygous offspring every time without mistake. If the inbreeding rate were lower or the number of heterozygous genes were less, selection would have more chance to alter the consequences of inbreeding. Actually, with each animal heterozygous for scores of genes, many of which have only minor effects which may be blurred by the effects of environment, the difference between intense selection and no selection under self-fertilization has little more effect on the outcome than the fate of a man dropped into the Niagara River just a few yards above the falls would be affected by whether he is a good swimmer or a poor swimmer! The difference in swimming ability might be of tremendous importance if he were in comparatively still water, as is roughly analogous to the situation in a population in which the inbreeding is very mild, but would only rarely make a detectable difference in the results in the presence of the much more powerful force of the swiftly moving water.

Copy Self-fertilization is impossible in the higher animals, but the Mendelian basis of the inbreeding effect may be illustrated with the continued inbreeding of full brother and sister. For each allelic set of genes this constitutes a population of four genes—two in the sire and two in the dam—from which four are to come to constitute the next generation. Gene frequency can have only the values: .00, .25, .50, .75, or 1.00. Although only one of them will occur in any one generation in any one line, six different types of matings are possible. Those types are:

Type	Mating	Frequency of A in this inbred line
1	$AA \times AA$	1.00
2	$AA \times Aa$.75
3	$AA \times aa$.50
4	$Aa \times Aa$.50
5	$Aa \times aa$.25
6	$aa \times aa$.00

If either the first or the last of these prevails, that line will remain homozygous for that gene indefinitely, unless a mutation occurs. If either the second or the fifth type prevails in one generation, there is one chance in four that this line will become homozygous in the next generation, two chances in four that it will remain the same, and one chance in four that the next generation will be like the fourth type of mating. When the line is of the third type, it will change to the fourth type in the next generation. When it is of the fourth type, there is one chance in eight that it will become homozygous in the next generation,

four chances in eight that it will change to types two or five, one chance in eight that it will change to type three, and two chances in eight that it will remain the same. Once the inbred line becomes type one or type six, it remains that way. It can shift back and forth among the other four types; but from them it will occasionally drift into types one or six, from which it cannot return. Hence the ultimate end of all such lines would be type one or type six if the inbreeding were continued long enough. The drift from one type to another is so rapid in a population as small as a line inbred full brother by sister that, after the inbreeding gets well under way, nearly one-fifth of all the genes which are still heterozygous in the line at any given time become homozygous in the next generation. In larger populations the gene frequency would fluctuate less extremely, but in any finite population it would do some shifting. Inbreeding is only an extreme form of a process which exists to some degree in all populations. The fact that the number of breeding individuals in the population is finite permits gene frequency to vary because of the sampling which takes place when the genes of one generation are replaced by the genes of the next.)

This Mendelian proof of the nature of the inbreeding process was studied as long ago as 1914 by Fish, Jennings, and Pearl,¹ but it becomes extraordinarily difficult to follow even for regular inbreeding systems milder than full brother by sister and practically impossible to follow in the irregular inbreeding which occurs with farm livestock. Wright in 1921 published a generalized explanation of the consequences of milder forms of regular inbreeding and of irregular inbreeding. In 1931 he generalized this still further to establish the identity of the inbreeding effect and the general consequences of finite population size, even in cases which we would not ordinarily call inbreeding.²

By changing heterozygotes to homozygotes, inbreeding brings to light many of the recessive genes which would otherwise remain hidden. Most recessive genes have less desirable effects than their alleles. Inbreeding, therefore, usually lowers the average outward merit of the inbred animals. Inbreeding permits more rapid improvement of the breed by getting the recessive genes out from the shelter of their dominant alleles so that they can be found more readily. For example, if 1 per cent of the calves in the Aberdeen-Angus breed are now born red and the breeders were all to begin suddenly to inbreed as intensely as mating parent and offspring or full brother and sister, the percentage of red calves would in the first generation of inbred calves go up more than threefold. The distribution of the genotypes before and after the inbreeding would be as follows:

¹ *Amer. Nat.*, 48:57-62, 491-94, 693-96, and 759-61.

² *Genetics*, 6:124-43 and 16:106-29.

Before inbreeding: 81 % BB 18 % Bb 1 % bb
After one generation of inbreeding: 83½ % BB 13½ % Bb 3½ % bb

The percentage of heterozygosis would decrease one-fourth, the genes which would have been in heterozygous individuals now being equally divided among the two kinds of homozygotes. The gene frequency has not changed, but only the zygotic ratio. On account of dominance, the desirable increase in BB and decrease in Bb individuals would not be apparent outwardly. The only readily apparent change would be the threefold increase in the proportion of red calves.

For ages men have observed this general fact that inbreeding tends to produce a certain amount of degeneration or decline in individual merit. Formerly it was thought that the inbreeding in some mysterious way actually damaged the inheritance and thus directly caused this degeneration. Now it is understood that the inbreeding merely acts somewhat as a detective does in uncovering crime—not in creating it. The undesired recessive genes are there all the time, but homozygous recessive individuals appear more frequently when inbreeding begins.

More than any other breeding method, inbreeding tends quickly to separate the population into many distinct families, each of which is uniform within itself but distinct from others. This splitting of the population into distinct families offers more opportunity for selection between families than could take place in a random-bred population. Inbreeding without selection leads toward a variable population composed of unlike lines. If inbreeding were carried to completeness without selection, the composition of the resulting population would be the same as if the gametes from the initial population had suddenly been transformed into zygotes by doubling all their chromosomes. If all the genes acted only in an additive way, the genetic variance in the new entirely homozygous population would be exactly twice what it was in the original random-bred population, but would be entirely between families, with no genetic variance within families. If many of the lines were discarded, the population as a whole might then become more uniform than it was before the inbreeding began; but that would be primarily the result of discarding the poorer inbred lines rather than a result of the inbreeding itself.

Inbreeding is especially powerful in forming families because the genetic likeness of the mates does not depend upon the breeder's ability to recognize which animals have similar genes when he mates them together, as is the case with selection and with assortive mating. The effects of inbreeding are not limited by the breeder's mistaking the effects of environment, dominance, or epistasis for the effects of genes,

as the effects of those other breeding methods are. That is why inbreeding is particularly powerful and useful in breeding for characteristics which are only slightly hereditary. This difference also leads to the general situation that under an inbreeding system the mates are more alike in their heredity than they are in their appearance, whereas under assortive mating they appear more like each other than they really are. Where the correlation between genotype and phenotype is low, this difference may be extreme.

Inbreeding may also produce some degeneration of individuals by scattering the genes which in certain combinations produce a desirable effect but which separately produce neutral or undesirable effects. If there really is much of this epistasis, and if a breed has been under strict selection for some time, there will have been a tendency to bring together, in combinations where they will show good effects, those genes which stick together well. Since most of those combinations will still be heterozygous, at least for some of the genes concerned, any inbreeding will tend to separate those combinations again and thus will lead to some apparent loss of individual merit in addition to that coming entirely from uncovering recessives.

Also inbreeding will lower the average merit of the population directly by reducing heterozygosity among those pairs of genes in which the heterozygote is more desirable than either homozygote.)

MEASURING THE INTENSITY OF INBREEDING

Since the primary effect of inbreeding is to increase the probability of receiving duplicate genes from sire and from dam, the measure of inbreeding ought to be one which shows how much decrease in heterozygosity is to be expected from that particular kind of inbreeding. Such a coefficient will mean little so far as concerns one pair of genes in one animal, but it may tell much about the average condition of one pair of genes in a whole herd or breed, and it will tell much about the average heterozygosity of the whole group of genes in an individual animal.

There seems to be no possibility that we shall ever be able to count the actual number of heterozygous genes in each animal. Each animal must be compared with the average condition in the population chosen for a base. The most convenient population to use for a base in animal breeding is usually the breed at the date to which the pedigrees are traced. It is then assumed that those foundation ancestors were a random sample of the breed at that date. Occasionally that assumption may lead to some error, when a pedigree if traced another generation or two would have revealed that the foundation ancestors were highly related to each other.

The inbreeding coefficient (devised by Wright³) starts at zero for random mating, in which case the probable proportion of heterozygosity is $2q(1-q)$, and increases toward 100 per cent as the probable proportion of heterozygosity goes toward zero. The inbreeding coefficient has to be expressed relatively rather than in terms of the actual number of heterozygous genes. For example, if the average Shorthorn of 1910 was heterozygous for 200 pairs of genes, then a Shorthorn, so bred that its inbreeding coefficient is 25 per cent relative to 1910 as a base date, will probably be heterozygous for only 150 pairs of genes. On the other hand, if the average Shorthorn in 1910 was heterozygous for a thousand pairs of genes, a Shorthorn showing an inbreeding coefficient of 25 per cent would probably still be heterozygous for about 750 pairs. An inbreeding coefficient of 25 per cent in one breed may not mean the same number of heterozygous genes as an inbreeding coefficient of 25 per cent in another breed. This need not bother us, since we really take that into account at the start when we recognize that the one breed is more uniform than the other.

The inbreeding coefficient of an individual is exactly one-half the relationship between its parents unless those parents are themselves inbred, in which case some correction (usually small) for that is to be made. The formula is as follows:

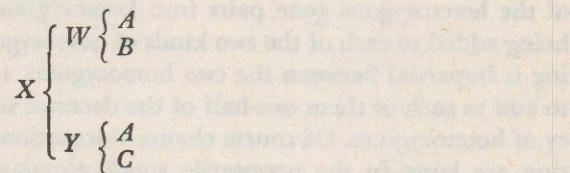
$$F_x = \frac{1}{2} \Sigma [(\frac{1}{2})^n (1 + F_A)]$$

where F_x is the inbreeding coefficient of animal X; n is the number of generations (the intervening segregations) in a line by which sire and dam are related; F_A is the inbreeding coefficient of the common ancestor (A) out of whom that line of descent divides; and Σ is the summation sign meaning that each such path of relation between sire and dam is to be evaluated separately and then all the results are to be added together. The $\Sigma[(\frac{1}{2})^n]$ part is exactly the formula discussed in the preceding chapter for relationship when no inbreeding is involved. Thus, when the parents are not inbred the inbreeding of the offspring is exactly half of the relationship of its parents to each other. The factor $(1 + F_A)$ corrects for the fact that, because an inbred ancestor (A) is probably homozygous for more pairs of genes than a random-bred ancestor, two gametes coming out of it will usually be alike in more of their genes than two gametes from a non-inbred ancestor. As a numerical example,

³ *Amer. Nat.*, 56:330-38 or *Jour. Heredity*, 14:339-48. A different measure of inbreeding had been proposed earlier by Pearl (*Amer. Nat.*, 48:513-28, 1914). It was based on a ratio between the number of different ancestors an animal actually had and the number it would have had if there had been no inbreeding. In general, it was a useful standard for comparing different intensities of inbreeding but in many cases gave inconsistent results. It is now of historical interest only, although references to it occasionally are made in current writings.

if a non-inbred ancestor is heterozygous for 200 pairs of genes, the average situation concerning two gametes from it is that they will have unlike genes in about 100 of those loci. From the same population an ancestor inbred 25 per cent would probably be heterozygous for only about 150 pairs of genes. Two gametes from it would be unlike in only about 75 loci. If the ancestor were complete inbred ($F_A = 1.0$, which can only be approached but not actually reached in farm animals), all the gametes from it would be exactly alike. This would be equivalent to eliminating one Mendelian segregation, and hence one 50 : 50 chance of unlikeness, from each line of relationship between sire and dam through this ancestor.

As a Mendelian example of why the formula for the inbreeding coefficient takes the form it does, consider the case of X , a double grandson of A , with pedigree as follows:



W and Y are related to each other 25 per cent, and $F_X = 12.5$ per cent or $\frac{1}{8}$. The one line of descent connecting W and Y is $W \leftarrow A \rightarrow Y$. To see what will probably happen to the genetic composition of X , we will consider a pair of genes, Rr , for which A is heterozygous. What is the probability that X is homozygous (RR or rr) through having received duplicate genes in this locus from A ? We are not interested in genes from B or C since, as far as the pedigree shows, they are unrelated to each other or to A , and our inbreeding coefficient measures only how many of the genes heterozygous in the foundation animals (those at the base date to which the inbreeding was computed) have probably become homozygous in X because of its inbreeding. W and Y are each equally likely to have received R or r . They each are equally likely to transmit whichever gene (R or r) they did receive from A , or the allele to it which each received from its other parent. The probabilities with respect to the genes of the Rr pair in X are as follows:

- 4 chances in 16 that neither gene came from A .
- 4 chances in 16 that R came from A but the other allele came from a grandam.
- 4 chances in 16 that r came from A but the other allele came from a grandam.
- 2 chances in 16 that both genes came from A and X is Rr .
- 1 chance in 16 that both genes came from A and X is rr .
- 1 chance in 16 that both genes came from A and X is RR .

If either of the last two events happened, X is homozygous for a gene for which A was heterozygous. Together the last two events have a probability of one-eighth of happening. When we say that the inbreeding coefficient of X is $\frac{1}{8}$, we are saying that X is probably homozygous for $\frac{1}{8}$ of the genes which were heterozygous in the ancestors at the foundation or base date to which the pedigree of X was traced. If we combine the probabilities of each of the above events happening, and include also what would have happened if A had been RR or rr , we find that if many are bred like X (i.e., with the inbreeding that results from being double grandsons) from a population of grandparents whose zygotic frequencies are: $q^2RR : 2q(1-q)Rr : (1-q)^2rr$, then the most probable zygotic ratio among those bred like X is:

$[q^2 + Fq(1-q)]RR : 2q(1-q)(1-F)Rr : [(1-q)^2 + Fq(1-q)]rr$. In other words this amount of inbreeding will probably transform $\frac{1}{8}$ of the heterozygous gene pairs into homozygous ones, half of that $\frac{1}{8}$ being added to each of the two kinds of homozygotes. Thus the inbreeding is impartial between the two homozygotes, tending on the average to add to each of them one-half of the decrease it causes in the frequency of heterozygotes. Of course chance fluctuations concerning that fraction are large in the necessarily small population which is any one inbred line.

The measurement of inbreeding, even in the most complicated pedigrees, is simply computing the amount of heterozygosis probably lost because of the inbreeding. In the simpler cases, where sire and dam are related through only one or two lines, the computations are easy. It is only necessary to find the common ancestor, count and add the number of segregations between sire and ancestor and between dam and ancestor and compute $\frac{1}{2}$ to one higher power than that. If much of this is to be done, it is convenient to memorize or have handy a table of $(\frac{1}{2})^n$ for values of n from 1 to 7 or 9. When n is more than 6, this fraction is less than 1 per cent. Little is gained by investigating any one relationship too distant to contribute even this much, although if there are very many such lines, their total might be important.

In the more complicated cases it may be necessary and is convenient to draw the pedigrees in the arrow style shown in the middle and bottom of Figure 35. In this form of pedigree each ancestor is shown only once. An arrow leads from it to each descendant. Unless it had more than one descendant it did not provide any inbreeding itself, but merely transmitted to its one offspring some of the genes received from its parents. When pedigrees are drawn in arrow style it is usually easy to see at a glance what kind of a breeding system had been used and toward which ancestors the inbreeding had been directed. Printing

difficulties are an obstacle to using the arrow style widely, as well as the fact that in most pedigrees in sale catalogues and advertisements there is little or no inbreeding visible, and in many cases the owner does not wish to call attention to that small amount. At the bottom of Figure 35 are shown the computations for the amount of inbreeding coming from each line through which sire and dam are related.

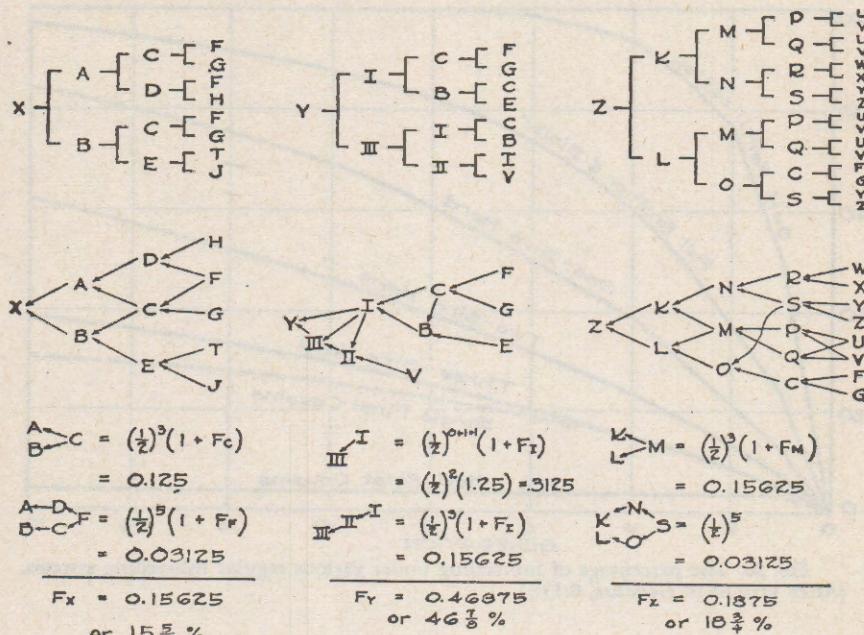


FIG. 35. Three pedigrees illustrating how the coefficient of inbreeding is computed.

In pedigrees from experiments where inbreeding has been conducted for many generations, the computations may become very intricate. Occasionally that happens in purebreeding where, as in the case of the "straightbred" Anxiety 4th Herefords, a family has been bred with little or no outside blood for more than five or six generations. For practical purposes it is usually sufficient in such cases to compute the inbreeding for only the last four or five generations and assume that the ancestors at that date were typical of this family, thus making the coefficient relative to this family at that date instead of making it relative to the whole breed.

Figure 36 shows for some regular inbreeding systems the sharp differences between the most intense systems theoretically possible and some of the milder ones which might more readily be practiced with farm animals. The milder inbreeding systems are much less intense at

the start but if continued long enough in an entirely closed population can bring the population to a high degree of homozygosity. How very long that would be in terms of one breeder's lifetime can be seen by multiplying the number of generations in Figure 36 by two and one-half years in the case of swine, four or five years in the case of cattle and sheep, and ten or more years in the case of horses.

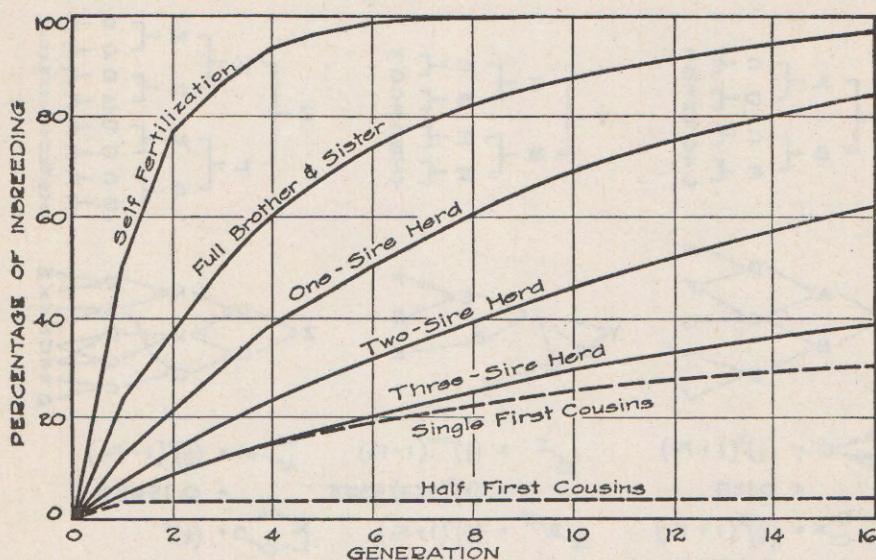


FIG. 36. The percentage of inbreeding under various regular inbreeding systems.
(After Wright in *Genetics*, 6:172.)

Figure 37 shows similarly what happens to the relationship between full brothers under the same inbreeding systems. Unrelated families are apt to drift farther apart under inbreeding than they would under random mating, but each tends to become uniform within itself. A one-sire herd where no females are ever purchased but each new sire is unrelated to the herd will approach but never rise above the level of an average relationship of $33\frac{1}{3}$ per cent between herd mates. By contrast a one-sire herd in which neither sires nor dams are purchased and there is no overlapping of generations will even in the first inbred generation reach an average relationship of 39 per cent between herd mates and in the next generation will pass 50 per cent. The whole herd will then be more uniform than if all members were full sibs.

THE RATE OF INBREEDING IN ISOLATED POPULATIONS

The complete formula for the inbreeding coefficient is unwieldy in estimating the consequences of any breeding plan which is to extend for

more than a few generations. For example, one might have a herd of cattle just big enough to justify keeping two sires at a time; and he might plan to raise his own sires without ever introducing any new stock from other herds. Soon his sires would be related to all the females on which they were to be used, but this relationship would vary. Many would be half sisters, some would be cousins, some would be less closely

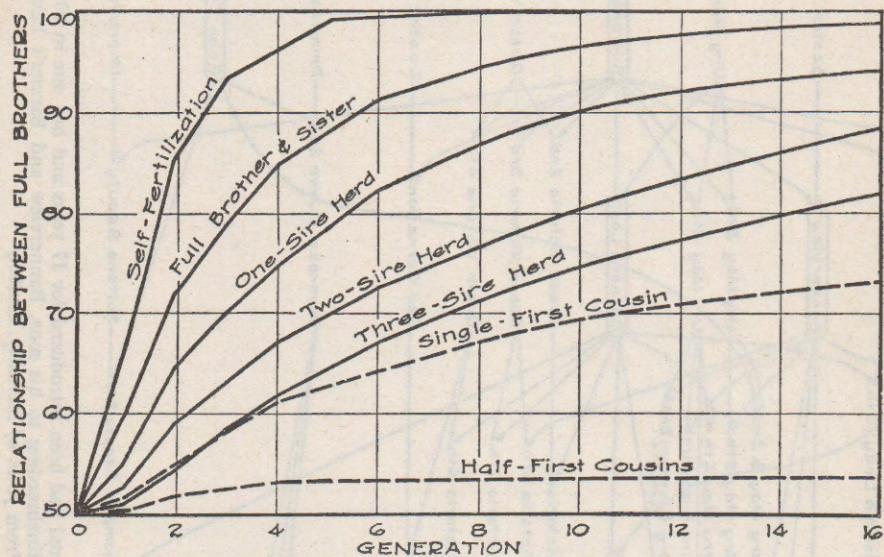


FIG. 37. The relationship between full brothers under various regular inbreeding systems. (After Wright in *Genetics*, 6:170.)

related older cows from the preceding generations, a few might be full sisters, dams, three-quarter sisters, etc. Figure 38 shows an actual example of this from a Shorthorn herd where only one sire and no females had been bought in 20 years.⁴ To compute the average inbreeding in such an actual herd after it has been produced is a tedious job and not very practical, since the animals are already produced whether one likes them or not. For practical purposes one wants to estimate and compare the consequences of various possible plans, so that the one thought most favorable can be adopted and the less favorable ones left untried.

If a population is kept entirely closed to outside blood, about $\frac{1}{8M} + \frac{1}{8L}$ of the remaining heterozygosity will be lost per generation, where M is the number of males and L is the number of females reach-

⁴ *Jour. of Heredity*, 25:208-16.

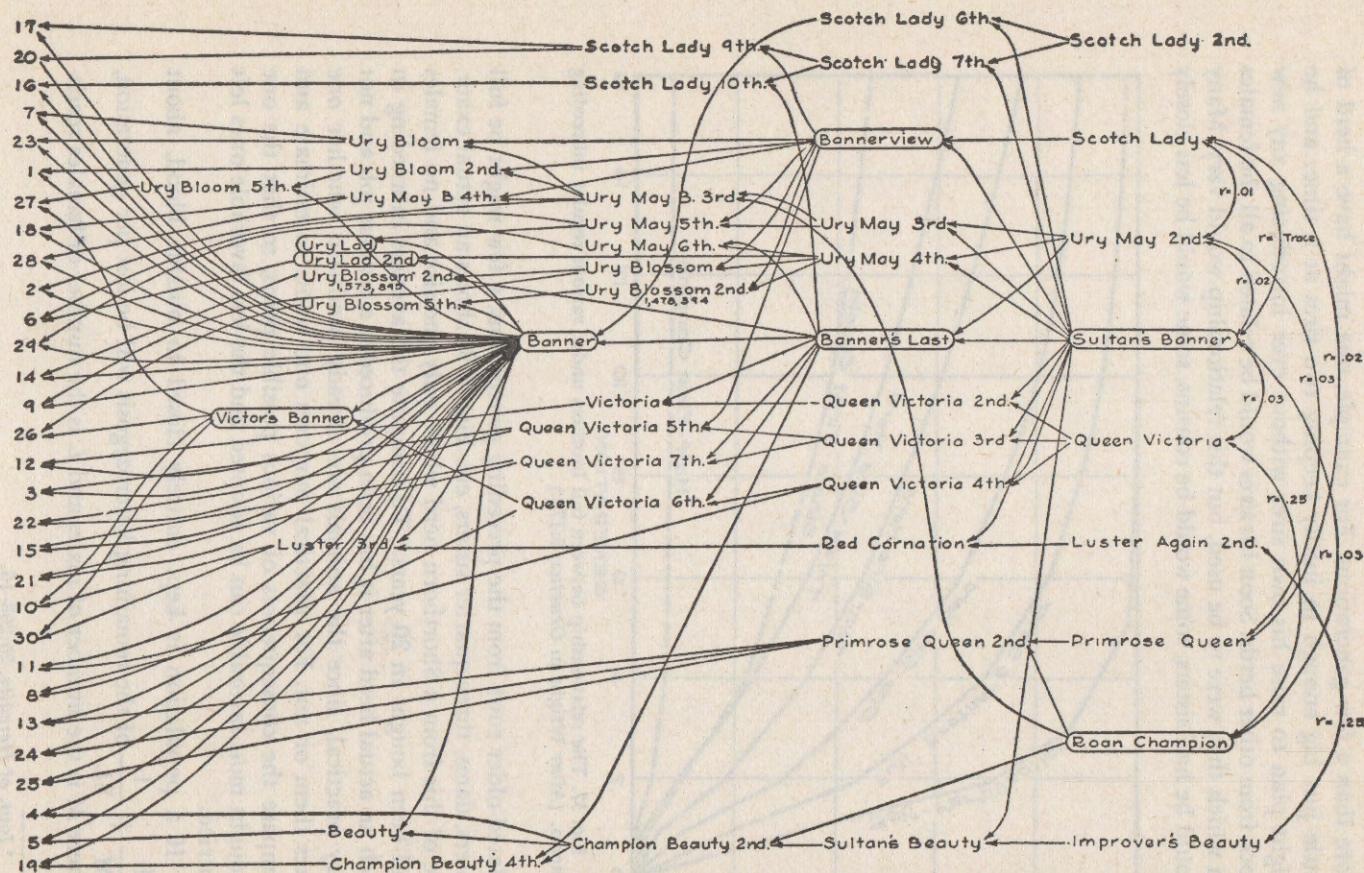


FIG. 38. Pedigree of a Shorthorn herd in which no animal had been introduced for 17 years and but one in 20 years. The herd was built largely around Sultan's Banner with some secondary linebreeding to his sons, Bannerview and Banner's Last and quite a bit of secondary linebreeding to his double grandson, Banner. (From *Jour. of Heredity*, 25:208.)

ing breeding age in each generation.⁵ In a herd where there are 2 sires and 40 females in active use, this would be $1/16 + 1/320$, or about 6.6 per cent of the remaining heterozygosity. In animal breeding, L will usually be so much larger than M that the term $\frac{1}{8L}$ can be neglected

without much error. Then the formula becomes simply $\frac{1}{8M}$ giving inbreeding rates of 12 per cent, 6 per cent, 4 per cent, and 3 per cent per generation, respectively, for one-sire herds, two-sire herds, three-sire herds, and four-sire herds, closed to all outside blood. These rates can be reduced somewhat by avoiding inbreeding as far as possible under those conditions. No reduction at all could be produced in a one-sire herd, only a small reduction in a two-sire herd, more in a three-sire herd, etc. The maximum effect of avoiding all inbreeding as far as possible within a closed population tends toward halving the rate given by the formula.

By this formula we can calculate where purebred systems with rigidly closed herdbooks are drifting, so far as concerns any inbreeding which is inevitable because the members of a pure breed are becoming more closely related to each other. Even in a small breed with 200 sires and 2,000 dams used per generation, the formula shows only .069 per cent of the heterozygosity lost per animal generation. In other words it would take about 15 animal generations to lose 1 per cent of the remaining heterozygosity in such a small breed. There need be no fear that a closed herdbook will automatically lead to dangerously high inbreeding, even though the herdbook remains closed and the breed remains moderately small for centuries. However, show rings, advertising, and other sales efforts make some males more popular than others. These males have many sons and grandsons which go to head other registered herds. Less popular sires have no sons which see service in purebred herds and perhaps few daughters and no grandsons. This has the effect of making M in the formula much smaller than the actual number of males which have registered daughters in each generation. In several pure breeds so far studied, the decrease in heterozygosity per generation on account of the inbreeding practiced is not very far from 0.4 to 0.6 per cent. Even so, only about 10 to 12 per cent of the present amount of heterozygosity would disappear in another century of pure breeding like

⁵ For the derivation of this formula see: *Genetics*, 16:107-11. Strictly speaking, M and L are the "effective numbers." They would equal the actual census numbers in the simple case in which all males and all females had equal chance to leave offspring. Many conditions can cause the effective numbers to be smaller than the actual numbers. At least a few of these will occur in practice. Hence the formula will underestimate the amount of inbreeding in closed populations. See *Amer. Nat.*, 74: 241-47. 1940.

that of the last 30 years. An occasional undetected fraudulent registration of a grade would further reduce this rate.

COMPLETE FORMULA FOR THE MEASUREMENT OF RELATIONSHIP

The measures of relationship can now be corrected for the effects of inbreeding. The complete formula for the coefficient of relationship between animals X and Y is:

$$R_{XY} = \frac{\sum [\frac{1}{2}^n (1 + F_A)]}{\sqrt{1 + F_X} \quad \sqrt{1 + F_Y}}$$

where n is the total number of Mendelian segregations in the path of descent through which X and Y are related. This differs from the approximate formula used in the last chapter only by having terms for the inbreeding of X and Y and of their common ancestor. The $(1+F_A)$ in the numerator allows for the fact that an inbred ancestor (A) is homozygous for more pairs of genes than a non-inbred one. Its use is illustrated in Figure 35 where the inbreeding of I adds to the relationship between itself and III, or the inbreeding of M increases the relationship between K and L . The terms in the denominator are to correct for the fact that inbreeding makes the population more variable, the inbred lines tending to drift apart from each other. Relationship is a fraction which has for its numerator the number of genes in which the two related animals are probably alike but which would be unlike in two random animals from the base population, and for its denominator the average number of genes in which two animals probably would be unlike if they were unrelated but descended from the base population by the same kind of breeding system as the two actually are. The denominator grows larger with their inbreeding because the inbreeding tends to decrease the proportion of heterozygosity and to throw the population toward the two homozygous extremes in each pair. In a highly inbred population two unrelated individuals (necessarily from different inbred lines if they are unrelated) have a considerably larger chance of being AA and aa than if they were from a non-inbred population, because in the inbred population there are more AA and aa and fewer Aa individuals present. This increase in the denominator naturally lowers the relationship unless there is a corresponding or greater increase in the numerator. Such an increase in the numerator can and usually does occur if the two animals are members of the same inbred line but not if they belong to lines which have separated and no longer interbreed with each other.

The complete formula for relationship between an animal and its

ancestor where there is no collateral relationship may be written

$$R_{XA} = \Sigma [\frac{1}{2}^n] \sqrt{\frac{1 + F_A}{1 + F_X}} = \text{"Percentage of blood" times } \sqrt{\frac{1 + F_A}{1 + F_X}}$$

If A and X are equally inbred, the term under the square root sign equals 1.0 and the percentage of blood is exactly equal to the coefficient of relationship. If the ancestor is more highly inbred, the figure for percentage of blood is not quite large enough. This is because there will be more than the average number of cases in which the ancestor is homozygous and therefore *both* its genes in that pair will be like the one its descendant receives from it. If the descendant is more highly inbred, the figure for percentage of blood is a little too large. This is because there will be cases in which the descendant is homozygous for a gene heterozygous in the ancestor. In such gene pairs the descendant gets 100 per cent of its genes from that ancestor and yet is not 100 per cent like the ancestor. For an example we may return to the pedigree of X (page 273) which was a double grandson of A . In one-fourth of the cases for any one pair of genes, X gets both its genes from the grandams and none from A ; in one-half the cases, X gets one gene of the pair from A and the other from a grandam; in the remaining one-fourth of the cases, X gets both genes from A . On the average, therefore, X gets 50 per cent of its inheritance from A , just as the percentage of blood figure shows. However, in the one-eighth of the cases when X is rr or RR , it will get both genes from A but yet will not be exactly like him, because he was Rr . The corrections in the denominator thus keep the relationship coefficient a measure of probable genetic likeness and not merely a measure of source of the genes, as is percentage of blood. Not often is the difference in the inbreeding of A and X large enough to be important. A much more serious general defect of percentage of blood as a measure of relationship is that it does not include collateral relationship and that collateral relationship cannot readily be measured by any way of manipulating percentage of common blood.

In the pedigrees ordinarily encountered in actual animal breeding, the denominator of the relationship coefficient does not get very much larger than 1.0. Neglecting it altogether is not apt to lead to a serious mistake. However, it must be included if the formula is to be entirely correct. It is not often worthwhile to carry the computation of either R or F for individual animals farther than to the nearest 1 per cent. Often the nearest 5 per cent is close enough. The sampling variations inherent in Mendelism prevent one from being sure that the computed coefficient describes with extreme accuracy the actual situation in individual cases, even if one could make practical use of small differences in these coefficients.

The similarity between the formula for inbreeding and the complete formula for relationship shows how it is that an individual's inbreeding depends upon the relationship between its sire and its dam. The equations connecting the two, where *S* represents the sire, *D* the dam, and *O* the offspring, are:

$$F_O = \frac{R_{SD}}{2} \times \sqrt{(1 + F_S)(1 + F_D)}, \text{ and } R_{SD} = \frac{2F_O}{\sqrt{(1 + F_S)(1 + F_D)}}$$

Unless the sire and dam are highly inbred, the term under the square root sign will not differ much from 1.0; and it will be approximately correct to say that the inbreeding of the offspring is one-half of the relationship between its parents. This rule is useful when estimating the amount of inbreeding danger in a mating before that mating is made.

OTHER PROCESSES WHICH CAN AFFECT HOMOZYGOsis

The inbreeding coefficient expresses probable changes in homozygosity based on no other assumptions than that inheritance is Mendelian and is equal from the two parents. It neglects sex-linkage and the small changes in homozygosity which may be made by mutation and selection and by assortive mating which is not inbreeding.

So far as concerns sex-linked genes, the inbreeding coefficient for the pedigree of a heterogametic animal has no meaning. The heterogametic parent behaves as if it were entirely homozygous for sex-linked genes in transmitting to its homogametic offspring, and transmits no sex-linked genes at all to its heterogametic offspring. Referring for convenience to the female as the homogametic sex (as is correct for the mammals but not for the birds and a few other animals), the inbreeding computed for a female's pedigree is not true for her sex-linked genes wherever the line of descent is from sire to son. On the other hand, wherever the line of descent is from sire to daughter, the homozygosity of females for sex-linked genes will be higher than the coefficient indicates. These two effects tend partly to cancel each other so that the inbreeding coefficient will generally measure the extra homozygosity of females, even for sex-linked genes. There will be cases where the coefficient will be systematically in error for the sex-linked genes; e.g., a double granddaughter of a male would not tend to have her sex-linked genes any more homozygous than if her parents had been unrelated, while a double granddaughter of a female would have her sex-linked genes 25 per cent less heterozygous instead of the expected 12½ per cent.⁶

⁶A more detailed explanation of the consequences of inbreeding on the distribution of sex-linked genes was presented by Wright in 1933. *Proc. Nat. Acad. Sci.*, 19:411-20.

Mutation is so rare an event that its neglect in the formula introduces no error of importance in practical breeding, although mutation needs to be included in evolutionary considerations where the time involved extends over an enormous number of generations. The formulas for including it are rather intricate.⁷

Selection affects homozygosity only incidentally through changing q and thereby the value of $2q(1-q)$. Selection will usually require many generations to make large changes in q , except in those cases where intense selection is directed at a characteristic the main variations of which are highly hereditary and are determined by a very few genes. The effects of selection on homozygosity certainly need to be considered in connection with problems of evolution, but in general they are probably too small to make inbreeding coefficients much in error as measures of the change in homozygosity which has occurred within the last four to six generations. Assortive mating (as will be explained in chapters 27 and 28) has almost no effect on homozygosity except when (1) the assortive mating is almost perfect, (2) the characteristics concerned are highly hereditary, and (3) the number of genes producing the observed variation is small. Very rarely would all these conditions be met in actual practice.

PRACTICAL USES OF INBREEDING

(Most breeders inbreed only when they must to attain some other object, such as linebreeding or forming and preserving family distinctness. The commonest reason for inbreeding is that a breeder must do some of it if he is to keep his animals closely related to individual animals he admires. Relationship between two animals cannot go higher than 50 per cent unless there has been some inbreeding. If a breeder continually uses unrelated sires, the relationship of each succeeding generation to the animals he has had in his herd will be halved. In a short time his animals will be very little related to the best ones of two or more generations ago. If he still has a good herd, that will be because he has been successful in selecting his subsequent sires. If, instead of using unrelated sires each generation, he uses sires closely related to the best animals he has had, then he may keep the future generations as closely related to those good ancestors as his present animals are. But, since both sires and dams of his stock are related to these good animals, he will be practicing some inbreeding. This is the essence of "linebreeding," which is the subject of Chapter 23. In this practice most breeders regard inbreeding as a necessary evil which must be endured if they are to keep their herd closely related to some noted animal, but which

⁷ *Genetics*, 16:116-37.

should be kept as low as can be done and still accomplish the linebreeding program.

If the homozygous recessives can all be discarded, inbreeding can be a powerful help to selection against rare recessives. There may be so many recessives in the stock that the inbreeding will bring them to light in more animals than the breeder can afford to discard, or he may not recognize some of those with the less conspicuous effects in time to discard them before they become fixed on his whole herd. This is what breeders have in mind if they say that their breed is not yet perfect enough to make even linebreeding wise as a general policy. The price which must be paid for using inbreeding thus to improve the breed is the occurrence at first of a larger proportion of undesirable individuals. That price may be so high that the individual breeder will not find it economically possible for him to practice extremely close inbreeding as a steady policy.

Inbreeding may be used to test whether animals are good enough to justify deliberate and long-continued attempts to keep the herd closely related to them. Inbreeding is the severest test of the hereditary worth of an individual that can be made. Wriedt goes so far as to recommend that every dairy bull thought worth using in the first place should be bred as soon as possible to enough of his daughters to insure that there will be at least 15 or 20 of his daughters out of his own daughters to prove his breeding value. For several reasons this proposal seems too extreme for general adoption. However, it does rest on the truth that inbreeding is the severest and quickest test to find whether an animal has any undesired genes.

Inbreeding can be used to promote homozygosity. Homozygosity has little commercial value in the sale ring as yet. Hence it seems unlikely that many breeders could afford to inbreed intensely just for this object. Nevertheless, homozygosity is the most important element in prepotency, and the building of this into his herd is worth some effort by the breeder, provided he can maintain or improve the average phenotypic merit at the same time.

A breeder often practices inbreeding merely for economy. This is an unwise policy whenever the animals are of only average merit. He could then expect only offspring of average merit, even if there were no inbreeding. With the added probability of some phenotypic degeneration from inbreeding, he can expect the offspring to be below the average merit of their breed as individuals, although not necessarily below the breed average in their merit as breeding animals. When the animal to which the inbreeding is being directed is of superior merit, this reason of economy lends additional weight to the argument for inbreeding.

One of the important general reasons for practicing inbreeding is that it tends to form distinct families within the breed and thus permits more selection between families than would be possible under random breeding. (This will be discussed in more detail in Chapter 24). Selection between families can be much more accurate than selection between individuals, especially for characteristics which are only slightly hereditary; but the families must be rather distinct from each other if that is to be the case. The family averages of non-inbred families do not deviate from each other as much as individual genotypes do.

The producer of market animals has little reason to practice inbreeding. His market will not pay him any extra for prepotency. Improvements he may make in the average merit of his own herd by using inbreeding along with selection will be about halved next time he buys an unrelated sire from some other source, as most commercial producers do. Economy can be a valid reason with him, especially when he thinks the sire he has is better than the next one is likely to be. Partly offsetting this superiority of his present sire is the probability that some harmful results of inbreeding will occur in his herd.)

THE DANGERS OF INBREEDING

Inbreeding makes desirable and undesirable genes homozygous impartially. If the rate of this is too rapid, every individual produced will be homozygous for some undesired genes as well as for some desired ones. If the inbreeding is too mild, many generations will be needed to accomplish much with it. The problem of the best rate at which to inbreed is one of keeping the inbreeding mild enough that the man in charge can avoid fixing the genes with undesirable effects and can fix as many as possible of the genes which have desirable effects. How mild or how intense such inbreeding can be depends upon several things, the most important of which are the skill of the man doing the selecting, the abundance of undesired genes in the stock with which he begins, the amount of linkage between desired and undesired genes in the initial stock, the amount of epistasis, dominance, or environmental effects which may deceive the breeder when he makes his selections, and whether he is breeding a group all by himself. If other men are breeding closely related lines, he can correct his mistakes by mild outcrosses to some of their herds without having to use totally unrelated animals.

Fragmentary evidence of various kinds indicates that inbreeding rates as high as 6 per cent per generation⁸ under favorable circumstances may be pursued for many generations without noticeably harmful consequences. It is unlikely that inbreeding rates as high as 3 or 4

⁸ As, for example, in a two-sire herd where no outside blood is introduced.

per cent can go on forever without harm, but certainly they can be continued for many generations. Many breeders when in possession of unusually good animals have had favorable results from mating half brother to sister or grandsire to granddaughters, but not many have continued to do that for more than two or three successive generations. Occasional matings of parent and offspring or, more rarely, full brother and sister have turned out well; but general experience is that those should be risked only when the stock is unusually good.

Among human beings inbreeding as intense as the marriage of first cousins has enough probability of undesired consequences that in some places it is forbidden by law or religious rule.⁹ Inbreeding more intense than that is regarded as "incest" in nearly all human societies although there have been some exceptions, as among the Pharaohs in ancient Egypt. No doubt the biological principles are the same in man as in other organisms, although the abundance of undesired recessives may be higher or lower. An extremely important practical difference is that in farm animals, if inbreeding brings to light a few more defectives than would occur without it, they may be culled with only the small economic loss that their defectiveness entails; whereas in most civilized communities of man the codes of ethics and morals do not permit such drastic action with defective human beings. The care and support of each one too defective to take care of itself is a serious burden, whether it is kept in a private home or in a special institution. Rigid prohibitions of marriages of a certain degree, such as between first cousins, do not allow for the fact that such marriages may be desirable when the common ancestry is of unusual merit. Prohibiting the marriage of relatives does not improve the average heredity of a population. Neither inbreeding nor outbreeding makes the undesired genes systematically either rarer or more abundant, but inbreeding does bring them together so that more of them can show their effects and be culled—if selection is being practiced. Perhaps the general experience of man over centuries may be considered as indicating that around 6 per cent is in general the "stop, look, and listen" level of danger from inbreeding? If the common ancestry is of sound stock, the children of such marriages may be above average in merit. If the common ancestry has any serious defect, even a rare one, the probability of that defect reappearing in the children who have a chance to inherit it from both sides is much higher than if their parents were unrelated. The rarer the defect in the general population, the more extreme is this difference.

⁹ See page 52 of *Time* for August 19, 1940, for a list of marriages forbidden by the Church of England in 1560. In 1945 prohibitions against ten of these categories of in-law marriages were removed. This was the first change in those rules in nearly four hundred years.

The inbreeding coefficient may be used to estimate the danger involved in any particular mating, if one considers also the merit of the ancestors from which the inbreeding comes. Inbreeding of 25 per cent coming from an outstanding ancestor might be safer than inbreeding of 10 per cent coming from a mediocre ancestor. Setting a definite percentage of inbreeding as the point where danger begins is much like setting a certain speed in automobile driving as the speed beyond which danger begins. In the case of the automobile much depends upon the condition of the highway, the field of vision, the mechanical condition of the car and the skill of the driver. Similarly with inbreeding, much depends upon the clearness of the goal, the accuracy of the tests and measures of merit, the initial scarcity of undesirable genes in the stock, the amount of culling which the reproductive rates permit, and the breeder's ability to recognize and discard genes which are on the verge of becoming fixed in his stock.

POSSIBILITIES OF PRODUCING INBRED LINES FOR COMMERCIAL CROSSING

Corn breeders have made a distinct success of producing inbred lines by self-fertilization and then crossing those lines which produce the most desirable crosses. The crossbred seed is sold for the production of commercial corn. Although the fundamental principles are the same, there are several differences in their application which make the success of such a breeding system appear less likely for animals than for plants, although modified systems based on the same principles may perhaps prove successful. In the first place, the closest possible inbreeding in animals is less than half as intense as self-fertilization. It would take many more generations with animals to reach the same degree of homozygosity. In the second place, the fertility of animals is lower than that of plants, so that not nearly as large a percentage of the individuals produced in each generation could be discarded. In the third place, the interval between generations in farm animals is longer than with annual plants; and the amount of time required to reach an equal degree of inbreeding would be longer for that reason also. In the fourth place, the individual animal is worth more money than the individual plant. Culling the undesired individuals which appear during the inbreeding will be more expensive than the same process applied to plants. In the fifth place, and partially offsetting these others, is the fact that the merits and faults of individual animals are usually better known than is the case with individual plants. Therefore, the individual selection which accompanies the inbreeding would be more accurate in animals. In the sixth place, the lower fertility of animals would make it economically difficult to sell the commercial producer as

many as he would need of the crossbred stock from two successfully inbred lines, if such should ever be produced, or to sell him inbred females of one line and inbred males of another line so that he could make his own crosses. Poultry and swine seem more nearly suited to the economics of that than the other farm animals.

For those reasons commercial animal breeding will never practice such intense inbreeding alternating with such extreme outbreeding as is already practiced in corn breeding. On the other hand, a mild form of this is already happening in the crossbreeding which is practiced for producing commercial meat animals and in the practice, among breeders of purebred stock, of making outcrosses between distinctly unrelated lines within a breed, hoping thereby to produce excellent individuals. Perhaps it may be commercially possible to produce highly inbred sires to be used on practically random-bred high grade or purebred females. At present stockmen set so much store by individuality in their sires that few of them would use inbred sires unless these were also good individuals, but that would change quickly if it were demonstrated clearly that such use would be profitable.

EXPERIMENTS ON INBREEDING

Thorough and extensive experiments on inbreeding have been more numerous with plants than with animals. Many of the facts about inbreeding were discovered in experiments with corn. More come from the contrasting behavior of naturally self-fertilized and naturally cross-fertilized plants when those are experimentally inbred or are used in various crosses. Conspicuous examples of plants which in nature have a high percentage of self-fertilization include wheat, cotton, sorghum and oats. Corn and beets are examples of naturally cross-fertilized species on which extensive experiments with inbreeding have led to the production of inbred lines and the sale of crossbred seed on a commercially important scale. Strawberries and raspberries show much the same results as corn and beets, but the application is different because vegetative multiplication of the former is practical.

Among animals, laboratory experiments have been extensive on the inbreeding of rats, mice, and guinea pigs. Dr. King inbred white rats full brother and sister for more than 70 generations without finding degeneration. Mice have been inbred full brother and sister in many experiments. In at least one case this has been carried further than the 55th generation.¹⁰ In the United States Department of Agriculture experiments on inbreeding guinea pigs, some lines have been inbred brother by sister for more than 30 generations. There have been several

¹⁰ *Jour. of Heredity*, 27:21-24, 1936.

short experiments on inbreeding chickens and swine at a number of experiment stations. In 1945 the 38 lines being studied in the Regional Swine Breeding Laboratory ranged from about 10 to 70 per cent in inbreeding. Twelve of them were already inbred more intensely than three generations of full brother by sister and ten more were nearly that far along. Inbreeding experiments with poultry at the Iowa Station have reached a more intense stage than that of nine generations of full brother by sister mating, although the breeding system actually used was not that regular.

In farm animals other than chickens and swine, the small number of full sibs and the variations in the sex ratio prevent the long-continued use of such regular inbreeding systems as full brother by sister. Even in chickens and swine these are serious difficulties and reduce tremendously the amount of selection which can be practiced while the inbreeding is being done. For the other farm animals the most intense inbreeding plan which can be followed long is the use of a sire on his daughters as long as he lives, he to be followed by one of his inbred sons, which in turn would be followed by one of his inbred sons, and so on. There would be a few full brother by sister matings and some of the females would live longer than others, some, perhaps, even outliving two generations of sires. Hence such a system of inbreeding would be far from regular, and there would be comparatively few pedigrees which were exactly alike in the kinds of inbreeding they showed over a period of three or four generations. Before an inbreeding coefficient was devised for measuring the intensity of the irregular inbreeding shown in these many kinds of pedigrees, it was natural that experimenters should think that inbreeding experiments of that kind could not be interpreted in any unmistakable way and therefore would not return scientific information worth the money and effort they would cost. Now that Wright's coefficient of inbreeding, which was first proposed in 1922, largely removes this objection, it is probable that more experimental study will be made of irregular systems of inbreeding.

Some of what we know about the results of inbreeding in animals comes from the scattered and irregularly reported experience of breeders. It is difficult to be at all sure that such evidence is a typical sample of the results of inbreeding. There is the question of whether the animals inbred were typical of purebred animals in general. There is also the question of whether one hears of the typical results of such cases or only of the exceptional results. Any bad result which does appear is apt to be blamed on the inbreeding in spite of the fact that equally bad results sometimes occur when no inbreeding is practiced. There is usually an absence of adequate control; that is, of non-inbred animals

kept under the same conditions. However, the results agree in general with those expected on theoretical grounds and with those actually obtained in laboratory experiments. The usual consequences of inbreeding in breeders' experiences is a degeneration which, however, is slight and irregular, affecting some characteristics in one animal and other characteristics in another and not affecting some individual animals at all. Even in Bakewell's time it was known and stressed that inbred animals are more apt to be prepotent and effective when used in outcrosses than are animals of equal individuality but not inbred.

The breeders who have practiced intense inbreeding for a long time have nearly always encountered enough degeneration that a cross with unrelated animals produced beneficial results. So universal has this experience been that breeders are rather generally convinced of the necessity of introducing "fresh blood" from time to time to "rejuvenate" a strain or herd. It is not always understood that this rejuvenating effect rarely occurs unless there has been some prior inbreeding. The explanation of these cases is that the herd becomes homozygous for undesirable genes which produce such small effects that the breeder scarcely notices them as they become fixed a few at a time, but instead just sees a gradual decline in vigor, fertility, size, etc. Since undesirable genes tend to be recessive, a cross with an animal from an unrelated herd often appears to remedy these defects at once.

SUMMARY

Inbreeding is the mating of animals which have a closer relationship to each other than the average relationship within the population concerned. Its measure is relative to some population, just as the measure of relationship is. Pure breeding is inbreeding relative to the whole species, but not many purebred animals are closely inbred relative to their breed.

The primary effect of inbreeding is to make more pairs of genes homozygous and to lower the percentage of heterozygosity correspondingly. Because this uncovers many recessive genes which would otherwise remain concealed by their dominant alleles, and because recessives generally have less desirable effects than dominants do, there is usually some degeneration in average individual merit when inbreeding is practiced.

Inbreeding does not of itself change gene frequency but does permit it to drift rapidly at random in each subgroup of the population.

Inbreeding is the most powerful tool the breeder has for establishing uniform families or strains which are distinct from each other. This it does by permitting gene frequencies to drift in different ways in different subgroups, by making the parents more homozygous, and by

providing more and more ways in which members of the same family are likely to inherit the same genes because their parents are related to each other.)

Some inbreeding is almost essential if selection is to have much success in those cases where a highly desirable effect is produced by a combination of genes which individually have undesirable effects; that is, for getting a population out of some of the lower "peaks of desirability" shown in Figures 20 and 21 and into higher nearby peaks.

The coefficient of inbreeding measures the percentage of genes which were heterozygous in the basic population but have probably become homozygous because of the inbreeding. It is subject to the sampling errors of Mendelian inheritance and hence means almost nothing for one pair of genes in one individual, but its sampling error may be small when it is applied to the average percentage of heterozygosity of one pair of genes in a whole population or to the average heterozygosity of the entire group of genes in one individual.

Among the more important reasons for practicing inbreeding are: (1) It is necessary if relationship to a desirable ancestor is to be kept high; (2) it helps uncover rare recessives so that they may be culled from the breed; (3) it forms uniform and distinct families so that interfamily selection may be possible in a more effective way than if inbreeding were not practiced; (4) it increases prepotency; and (5) it is sometimes economical, especially if the present sire is of such high merit that it will be difficult to find as good a one for a successor.

(The danger of intense inbreeding is that it will make undesired genes homozygous at so rapid a rate that it will be impossible to discard all individuals homozygous for them. Some of the undesired genes will therefore become "fixed" in the whole herd. The lowered sale value of the defectives uncovered by the inbreeding will cause some loss. From the standpoint of breed improvement, that loss is balanced by the increased prepotency of those which are not defective; but the man who is breeding animals for the commercial market will not receive that compensation.)

It seems reasonably certain that more opportunities for breed progress are lost by not inbreeding when inbreeding would be advisable than are lost by too much inbreeding. When inbreeding is too intense, the individual breeder may lose by that; but the progress of the breed is not apt to suffer. The best of the inbred animals are likely to give good results in outcrosses.

REFERENCES

The general subject of inbreeding was treated comprehensively in the following book, which, even a quarter of a century later, is obsolete

in little except its treatment of the measurement of inbreeding intensity:

East, E. M., and Jones, D. F. 1919. Inbreeding and outbreeding. Philadelphia: The J. B. Lippincott Co. 285 pp.

For explanation of the Mendelian basis of inbreeding and of what happens when various rates of inbreeding, mutation, and selection are balanced against each other, see:

- Wright, Sewall. 1921. Systems of mating. *Genetics*, 6:111-78.
- _____. 1922. Coefficients of inbreeding and relationship. *Amer. Nat.*, 56:330-38.
- _____. 1923. Mendelian analysis of the pure breeds of livestock. I. The measurement of inbreeding and relationship. *Jour. of Heredity*, 14:339-48.
- _____. 1923. Mendelian analysis of pure breeds of livestock. II. The Duchess family of Shorthorns as bred by Thomas Bates. *Jour. of Heredity*, 14:405-22.
- _____. 1931. Evolution in Mendelian populations. *Genetics*, 16:97-159.
- _____. 1940. Breeding structure of populations in relation to speciation. *Amer. Nat.*, 74:232-48.

For reports of actual experiments on inbreeding animals, see:

- Castle, W. E. 1930. Genetics and Eugenics, pp. 286-304. Cambridge: Harvard University Press.
- Hodgson, R. E. 1935. An eight-generation experiment in inbreeding swine. *Jour. Heredity*, 26:209-17.
- Hughes, E. H. 1933. Inbreeding Berkshire swine. *Jour. Heredity*, 24:199-203.
- King, Helen Dean. 1918 and 1919. Studies of inbreeding. *Jour. of Exp. Zoology*, 26:1-54, 26:335-78, 27:1-36, and 29:71-112.
- Strong, Leonell C. 1936. The establishment of the "A" strain of inbred mice. *Jour. Heredity*, 27:21-24.
- USDA Yearbook for 1936.
- Waters, N. F., and Lamhert, W. V. 1936. Inbreeding in the White Leghorn fowl. *Iowa Agr. Exp. Sta., Res. Bul.* 202.
- Willham, O. S., and Craft, W. A. 1939. An experimental study of inbreeding and outbreeding in swine. *Okla. Agr. Exp. Sta., Tech. Bul.* 7.
- Woodward, T. E., and Graves, R. R. 1933. Some results of inbreeding grade Guernsey and grade Holstein-Friesian cattle. *USDA, Tech. Bul.* 339.
- Wright, Sewall. 1922. The effects of inbreeding and crossbreeding on guinea pigs. I. Decline in vigor. II. Differentiation among inbred families. *USDA, Department Bul.* 1090. III. Crosses between highly inbred families, *USDA, Department Bul.* 1121.
- _____, and Lewis, Paul A. 1921. Factors in the resistance of guinea pigs to tuberculosis, with special regard to inbreeding and heredity. *Amer. Nat.*, 55:20-50.

For brief statements of breeders' experience with regard to inbreeding, see:

- Mumford, F. B. 1921. Breeding farm animals. pp. 217-42.
- Wriedt, Christian. 1930. Heredity in livestock. pp. 68-113.

For studies of the amount and kind of inbreeding which has occurred in various breeds of livestock, see:

- Berge, S. 1930. Inbreeding in Telemark cattle. (Translated title). *Nordisk Jordbruksforskning* 204-16.
- Brockelbank, E. E., and Winters, L. M. 1931. A study of the methods of breeding the best Shorthorns. *Jour. Heredity*, 22:245-49.
- Calder, A. 1927. The role of inbreeding in the development of the Clydesdale breed of horses. *Proc. Royal Soc. of Edinburgh*, 47, Part 2, No. 8, pp. 118-40.
- Carter, Robert C. 1940. A genetic history of Hampshire sheep. *Jour. Heredity*, 31:89-93.
- Dickson, W. F., and Lush, Jay L. 1933. Inbreeding and the genetic history of the Rambouillet sheep in America. *Jour. Heredity*, 24:19-33.

- Fletcher, J. Lane. 1945. A genetic analysis of the American Quarter Horse. *Jour. Heredity*, 36:346-352.
- _____. 1946. A study of the first fifty years of Tennessee Walking Horse breeding. *Jour. Heredity*, 37:369-373.
- Fowler, A. B. 1932. The Ayrshire breed: A genetic study. *Jour. of Dy. Res.*, 4:11-27.
- Lötscher, H. 1945. Inbreeding and relationship among the Jura horses today. (translated title). *Landw. Jahrb. d. Schweiz*, pp. 1-16.
- Lush, Jay L. 1946. Chance as a cause of changes in gene frequency within pure breeds of livestock. *Amer. Nat.* 80:318-342.
- _____, and Anderson, A. L. 1939. A genetic history of Poland-China swine. *Jour. Heredity*, 30:149-56 and 219-24.
- _____, Holbert, J. C.; and Willham, O. S. 1936. Genetic history of the Holstein-Friesian cattle in the United States. *Jour. Heredity*, 27:61-71.
- McPhee, Hugh C., and Wright, Sewall. 1925. Mendelian analysis of the pure breeds of livestock. III. The Shorthorns. *Jour. Heredity*, 16:205-15.
- _____. 1926. Mendelian analysis of the pure breeds of livestock. IV. The British Dairy Shorthorns. *Jour. Heredity*, 17:397-401.
- Rottensten, Knud. 1937. Inbreeding in Danish Landrace swine. (Translated title). *Nordisk Jordbruksforskning*, Hefte 8-4A, pp. 94-114.
- Sciuchetti, A. 1935. Ein Beitrag zur genetischen Analyse der schweizerischen Brauviehrasse. *Julius Klaus-Stiftung f. Vererb. Sozialanthr. u. Rassenh.*, 10:85-99.
- Smith, A. D. B. 1926. Inbreeding in cattle and horses. *Eugenics Review*, 18:189-204.
- Steele, Dewey. 1944. A genetic analysis of recent Thoroughbreds, Standardbreds, and American Saddle Horses. *Kentucky Agr. Exp. Sta., Bul.* 462.
- Stonaker, H. H. 1943. The breeding structure of the Aberdeen-Angus breed. *Jour. Heredity* 34:322-28.
- Willham, O. S. 1937. A genetic history of Hereford cattle in the United States. *Jour. Heredity*, 28:283-94.
- Yoder, Dorsa M., and Lush, Jay L. 1937. A genetic history of the Brown Swiss cattle in the United States. *Jour. Heredity*, 28:154-60.

CHAPTER 22

Prepotency

Prepotency is the ability of an animal to impress characteristics upon its offspring to such an extent that they resemble that parent or each other more closely than is usual. If the offspring are all unusually like this parent, they will naturally tend to be unusually like each other. Writings on animal breeding are full of references to prepotency. Many of those no doubt exaggerate the supposed amount of prepotency beyond the actual facts. Differences in prepotency do exist, however, and are sometimes large enough to be practically important.¹ Purebreds are usually more prepotent than crossbreds or grades. An animal may be prepotent for undesirable as well as for desirable characteristics, but naturally in breeders' discussions prepotency for desirable characteristics is mentioned more often.

"Potent" and "impotent" in animal breeding usage refer to the ability or inability of the animal to reproduce or even to copulate normally. These terms do not refer to the merit of the offspring.

GENETIC BASIS OF PREPOTENCY

Differences in prepotency depend mainly upon dominance and homozygosis. In some cases a part may be played by linkage and epistasis.

The most important cause of differences in prepotency is the degree of homozygosis in the animals concerned. A perfectly homozygous animal could produce only one kind of gamete. All its offspring would receive exactly the same genes from it. Any genetic differences between those offspring would depend entirely on their having received different things from their other parents. On the other hand, an animal heterozygous for n pairs of genes could produce 2^n different kinds of gametes. This permits its offspring to differ genetically, not only in what they received from their other parent, but also in what they received from the common parent.

Dominance is the other important cause of differences in prepo-

¹ Wentworth, E. N. 1926. Prepotence in character transmission. Proc. Scottish Cattle Breeding Conference for 1925, pp. 146-63.