INBREEDING

ITS MEANING AND USE IN ANIMAL BREEDING

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The various mating schemes are classified under two broad categories, *inbreeding* and *outbreeding*. Classification depends on the closeness of the biological relationship between mates. *Within* each category, there is a very wide variation in intensity of this relationship. *Between* the two categories, there is a very fine line. Everyone would undoubtedly agree that mating closely related animals (e.g., parent and offspring or full brother and sister) is inbreeding. With less closely related animals (half brother and sister, first cousins, second cousins, etc.), there is some diversity of opinion as to just where the line between inbreeding and outbreeding should be drawn.

Technically, inbreeding is defined as the mating of animals *more* closely related to each other than the average relationship within the breed or population concerned. Matings between animals *less* closely related than this, then, would constitute outbreeding. These two systems of mating, with varying intensities in each, are illustrated in Figure 1. Matings indicated within the category of inbreeding in this figure are self-explanatory; those within the outbreeding category may need explanation. *Outcrossing* is the mating of unrelated animals within a breed. *Breed crossing*, also commonly practiced, is the mating of animals of one breed to animals of another breed. Many *species crosses* have been made but are less common than breed crosses. One of the most well-known species crosses is the one that provided the genetic material for the development of the Santa Gertrudis breed of cattle. This involved crosses among beef-type Shorthorns (genus *Bos*, species *taurus*) and the American Brahman (genus *Bos*, species *indicus*). A number of genus crosses also have been made. Perhaps the most familiar of these are the crosses between domestic cattle (genus *Bos*) and the American Buffalo (genus *Bison*) to produce the "Cattalo."

Biological Relationship Between Animals

Individuals are considered to be biologically related when they have one or more common ancestors. For practical purposes, if two individuals have no common ancestor within the last five or six generations, they are considered to be unrelated.

Biological relationship has importance in animal breeding in that the closer the relationship the higher the percentage
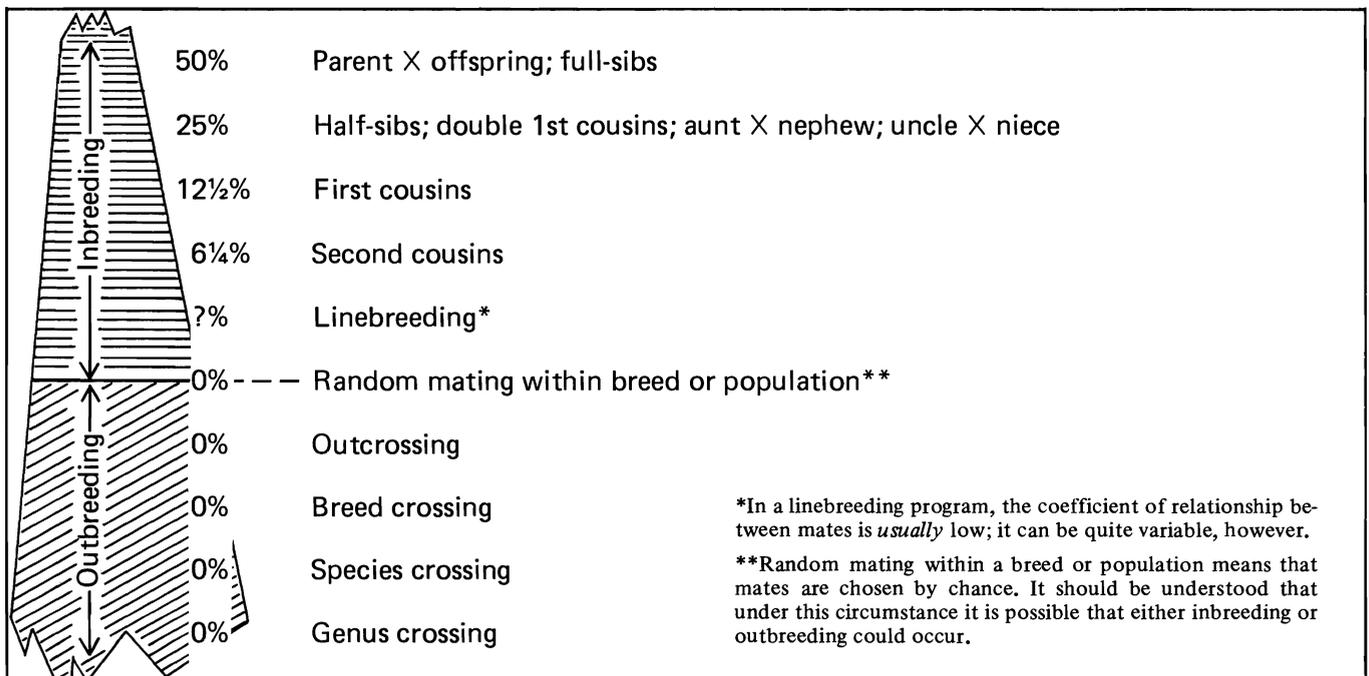
50%	Parent X offspring; full-sibs	
25%	Half-sibs; double 1st cousins; aunt X nephew; uncle X niece	
12½%	First cousins	
6¼%	Second cousins	
?%	Linebreeding*	
0% — — —	Random mating within breed or population**	
0%	Outcrossing	
0%	Breed crossing	
0%	Species crossing	
0%	Genus crossing	

*In a linebreeding program, the coefficient of relationship between mates is *usually* low; it can be quite variable, however.

**Random mating within a breed or population means that mates are chosen by chance. It should be understood that under this circumstance it is possible that either inbreeding or outbreeding could occur.

Figure 1. Degrees of inbreeding and outbreeding, arranged according to biological relationship between indicated mates. The number to the left of designated matings is the coefficient of relationship between mates. In reading from top to bottom, biological relationship between mates steadily *decreases*.

of like genes the two individuals carry. Closeness of relationship is indicated by how far back in the two animals' pedigrees the common ancestor appears, the number of common ancestors and how frequently each appears. It is also influenced by any inbreeding of the common ancestor or ancestors.

Measurement of degree of biological relationship. The coefficient of relationship is a single numerical value which considers all the above-mentioned factors and is a measure of the *degree to which the genotypes (genetic constitutions) of the two animals are similar.* It is estimated by the expression:

$$R_{BC} = \frac{\Sigma[(\frac{1}{2})^{n+n'}(1+F_A)]}{\sqrt{(1+F_B)(1+F_C)}} \quad \text{where,}$$

R_{BC} = the coefficient of relationship between animals B and C which we want to measure.

Σ = the Greek symbol meaning to add.

$(\frac{1}{2})$ = the fraction of an individual's genetic material that is transmitted to its progeny. It is used in the calculation of the coefficient of relationship because it represents the probability that, in any *one* generation, an identical gene from a given pair of genes is transmitted to each of two particular progeny. It is also the probability that an *unlike* gene from a given pair of genes is transmitted to the two progeny.

n = the number of generations between animal B and the common ancestor.

n' = the number of generations between animal C and the common ancestor.

F_A, F_B, F_C = inbreeding coefficients of the common ancestor and of animals B and C, respectively.

If none of the animals is inbred, the coefficient of relationship is estimated as

$$R_{BC} = \Sigma[(\tfrac{1}{2})^{n+n'}].$$

The use of this expression can be demonstrated with the full-sib sample pedigree and arrow diagram below. In this example, it is assumed that neither sire nor dam is inbred. The arrow diagram on the right shows paths of gene flow from each of the common ancestors (D and E) to the animals whose coefficient of relationship we are measuring (B and C).
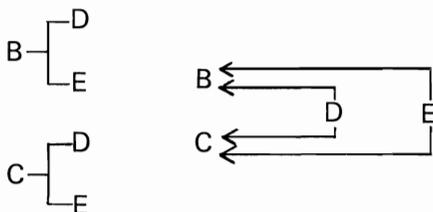
The problem now is to trace all possible paths from animal B to animal C which pass through a common ancestor. In this case, there are two such paths.

$$B \xleftarrow{\;n\;} D \xrightarrow{\;n'\;} C$$

$$B \xleftarrow{\;n\;} E \xrightarrow{\;n'\;} C$$
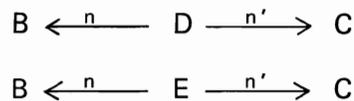
Since we have assumed no inbreeding in this example, the coefficient of relationship between animals B and C is estimated as:

$$R_{BC} = \Sigma[(\tfrac{1}{2})^{n+n'}] = (\tfrac{1}{2})^{1+1} + (\tfrac{1}{2})^{1+1}$$
$$= (\tfrac{1}{2})^2 + (\tfrac{1}{2})^2 = 0.50$$

Usefulness of coefficient of relationship information. There are a number of situations in which the livestock producer would find coefficient of relationship information of value. He may, for example, be considering selling an animal that is related to one which previously sold for a high price; the higher the coefficient of relationship between the two, the better would be its use as a sales point. Or, he may be considering the purchase of one of two related bulls, one of which is higher priced than he can afford or wishes to pay. If the coefficient of relationship between the two bulls is high, he would likely be as well off with the lower priced bull as he would with the more expensive one.

One of the most practical uses of the coefficient of relationship is in estimating the performance value of an untested animal. To accomplish this, we must know the performance value of a related animal, the coefficient of relationship between the tested and untested animals, and the average performance value of the breed, herd or group to which the tested and untested animals belong. As an example, consider a herd of beef cattle whose average feedlot average daily gain (ADG) is 2.25 lb/day. Assume further that a bull from this herd had a 3.50 lb/day feedlot ADG, while a younger half brother has, as yet, not been evaluated for feedlot ADG. Assuming no inbreeding, the coefficient of relationship between half brothers is 0.25. The best estimate of the untested bull calf's feedlot ADG is that it will deviate from the herd average 25 percent as far as does the performance value of the tested half brother. Using these figures, the most probably feedlot ADG value of the untested animal is 2.25 + (.25)(3.50 - 2.25) or 2.56 lb/day.

Measurement of the degree of inbreeding. When we calculate an inbreeding coefficient, we are attempting to measure the *probable percentage reduction in the frequency of pairing of dissimilar genes (reduction in heterozygosity).* This reduction is relative to a base population. The base population usually is the breed concerned at a date to which the pedigrees are traced. Animals in this base population are assumed to be non-inbred. This does not mean that these base population animals had dissimilar genes in each pair—there is no way for us to know how many of their gene pairs were constituted of similar genes and how many of dissimilar genes. The inbreeding coefficient that is calculated is simply relative to that base and reflects the probable percentage reduction in *however many dissimilar gene pairs* the average base population animals had.

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The general expression for determining the inbreeding coefficient is:

$$F_x = \Sigma [(\tfrac{1}{2})^{n + n' + 1}(1 + F_A)] \quad \text{where,}$$

F_x = the inbreeding coefficient of animal X.

Σ = the Greek symbol meaning to add (as before).

$(\tfrac{1}{2})$ = the fraction of an individual's genetic material that is transmitted to its progeny. It is used in the calculation of the coefficient of inbreeding because it represents the probability that, in any *one* generation, an identical gene from a given pair of genes is transmitted to each of two particular progeny. It is also the probability that an *unlike* gene from a given pair of genes is transmitted to the two progeny.

$+1$ = is added to n and n' to account for the additional generation between animal X and its parents.

n = the number of generations between animal B and the common ancestor.

n' = the number of generations between animal C and the common ancestor.

F_A = the inbreeding coefficient of the common ancestor.

If neither parent is inbred, but they are related, the inbreeding coefficient of their progeny is one-half their coefficient of relationship, $\tfrac{1}{2} R_{BC}$. This can be demonstrated using a full-sib mating to facilitate comparison with the full-sib coefficient of relationship calculated previously. In this case, the pedigree for animal X and the arrow diagram will be as follows:
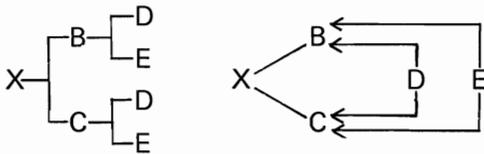
The problem now is to trace all possible paths from the sire (B) to the dam (C) through each common ancestor. As with the coefficient of relationship problem, there are two such paths.

$$X \longleftarrow B \xleftarrow{n} D \xrightarrow{n'} C \longrightarrow X$$

$$X \longleftarrow B \xleftarrow{n} E \xrightarrow{n'} C \longrightarrow X$$

Since we have assumed that neither parent is inbred, the inbreeding coefficient of animal X is estimated as:

$$F_x = \Sigma [(\tfrac{1}{2})^{n + n' + 1}] = (\tfrac{1}{2})^{1 + 1 + 1} + (\tfrac{1}{2})^{1 + 1 + 1}$$
$$= (\tfrac{1}{2})^3 + (\tfrac{1}{2})^3 = 0.25$$

which is one-half the coefficient of relationship between full-sibs when there is no inbreeding.

Genetic consequences of inbreeding. The basic genetic consequence of inbreeding is to promote what is technically known as *homozygosity.* This means that there is an *in-crease in the frequency of pairing of similar genes.* Accompanying this increase, quite obviously, there must be a *decrease in the frequency of pairing of dissimilar genes.* This is called a decrease in "heterozygosity." These simultaneous events (increase in homozygosity and decrease in heterozygosity) are the underlying reasons for the general effects on performance that we observe with inbreeding.

Reasons for inbreeding. Development of highly productive inbred lines of domestic livestock is possible. To date, however, such attempts have met with little apparent success. Although *occasional* high performance animals are produced, inbreeding generally results in an overall reduction in performance. This reduction is manifested in many ways. The most obvious effects of inbreeding are poorer reproductive efficiency including higher mortality rates, lower growth rates, and a higher frequency of hereditary abnormalities.

The extent of this decrease in performance, in general, is in proportion to the degree of inbreeding—the greater the degree of inbreeding, the greater will be the reduction in performance. The actual reduction in performance relative to the degree of inbreeding is not the same in all species of animals or in all traits. Some characteristics (like meat quality) are very little influenced by inbreeding; others (like reproductive efficiency) are very much influenced by inbreeding. One cannot, then, make a generalized statement as to the *amount* of reduction in "performance" which would result from a specific amount of inbreeding and expect it to be applicable in a broad variety of situations. It is possible, however, to predict the extent of the effect of inbreeding on *specific* traits. Such predictions are based on results actually obtained under experimental conditions in which various levels of inbreeding had been attained. In a summary of inbreeding research with swine conducted within the midwest regional swine breeding laboratory, Dickerson and others (1954) point out that, for each 10 percent increase in inbreeding (of the pigs in the litter), there is a *decrease* of .20, .35, .38, and .44 pigs per litter at birth, 21 days, 56 days, and 154 days, respectively. Such figures can be used to provide estimates of *expected* decreases in litter size (at comparable litter ages) in other herds of swine.

Most inbreeding studies suggest that each successive unit increase in inbreeding results in a proportional decrease in performance. Estimates of average increases in percentage inbreeding within a closed herd can be made with the expression,

$$\text{Avg. increase in inbreeding} = \frac{\text{No. males} + \text{No. females}}{(8)(\text{No. males})(\text{No. females})}.$$

In a closed herd of cattle in which 100 females and 4 males were used in each generation, for example, the average *per generation* increase in inbreeding would be $(4+100)/(8)(4)(100)=0.0325$. On a per year basis, assuming a generation interval of 5 years, this would amount to an average yearly increase in inbreeding of 0.0065 or 0.65 percent.

Despite the generally poor results obtained with inbreeding, it is a very useful tool in animal breeding. Inbreeding is essential to the *development of prepotent animals*—animals

that uniformly "stamp" their characteristics on their progeny. Because inbreeding causes an increase in the proportion of *like* genes (good or bad, recessive or dominant), the inbred animal's reproductive cells will be more uniform in their genetic makeup. When this uniformity involves a relatively large number of dominant genes, the progeny of that individual will uniformly display the dominant characteristics of that parent.

Inbreeding may also be used to uncover genes that produce abnormalities and/or death—genes that, in outbred herds, are generally present in low frequencies. These harmful genes are almost always recessive in their genetic nature and their effects hidden or masked by their dominant counterparts (alleles). Except for sex-linked traits, recessive genes are not expressed if carried singly—for their effects to be manifest, they must be present in duplicate. The likelihood that they will be present in duplicate is increased with inbreeding, since inbreeding increases the proportion of *like* genes (both good and bad) in the inbred population. With the effects of these genes uncovered, the breeder is in a position to eliminate them from his herd. To do this, he would need to cull the progeny that showed the undesirable effect of these recessive genes and also cull the parents that are carriers of the undesirable genes. In addition, two-thirds of the "normal" progeny of these carrier parents are themselves expected to be carriers of these same undesirable genes. In the absence of breeding tests to sort out the carriers from the noncarriers, it would also be necessary to cull all "normal" progeny of the carrier parents.

Another important use of inbreeding is in the development of distinct families or inbred lines. Beginning with an initially diverse genetic population, inbreeding results in the formation of various lines, each differing genetically from the other. Continued inbreeding within these lines tends to change the frequency of some of the genes found in the initial population. For example, if a particular gene is present in only 1 percent of the animals in the initial population, inbreeding and the development of distinct lines could result in this gene being present in all or nearly all animals in some lines and in none or only a few of the animals in other lines.

A mild form of inbreeding (linebreeding) is being used successfully by some commercial producers. Its objective is to maintain a high degree of relationship between the animals in the herd and some outstanding ancestor or ancestors. Linebreeding can be justified in high producing herds if the producer feels that, by going outside his herd for breeding stock, he would lower the herd's present level of production.

Summary

Inbreeding is technically defined as the mating of animals more closely related to each other than the average relationship within the breed or population concerned. For practical purposes, if two mated individuals have no common ancestor within the last five or six generations, their progeny would be considered outbreds. The primary genetic consequence of inbreeding is to increase the frequency of pairing of similar genes. All genetic and phenotypic changes associated with the practice of inbreeding stem from this one primary consequence. In general, inbreeding results in an overall lowering in performance. This reduction in performance is most obviously reflected in poorer reproductive efficiency, including higher mortality rates, lower growth rates, and a higher frequency of hereditary defects.

Despite these generally harmful effects, inbreeding is a very useful tool in the field of animal breeding. It enables the breeder to uncover and eliminate harmful recessive genes within the population. It is also essential to the development of prepotent animals and is desirable in the development of distinct family lines. In addition, commercial producers have successfully used a generally mild form of inbreeding (linebreeding) to maintain a degree of genetic relationship in their animals to some outstanding ancestor or ancestors.

Glossary of Terms to Describe Various Mating Schemes and the Progeny Resulting from Specific Mating Programs

Backcross—Progeny resulting from the mating of a two-breed cross animal to one of the parental breeds. For example, using two breeds designated as P_1 and P_2, backcross progeny would be produced by mating the two-breed cross animal (P_1 x P_2) with either of the P_1 or P_2 parental breeds.

Crisscrossing—A continuous program of crossbreeding in which there is an alternate use of males belonging to two breeds. Using two breeds designated as P_1 and P_2, a crisscrossing program, beginning with the two-breed cross animal (P_1 x P_2), would begin by backcrossing to one of the parental breeds [(P_1 x P_2) x P_1]. Females resulting from these matings would be bred to a P_2 male, [(P_1 x P_2) x P_1] x P_2, etc.

Crossbred—Progeny resulting from the mating of outcross animals belonging to different breeds.

Genus cross—Mating of animals belonging to different genera (e.g., mating of domestic cattle, *Bos taurus* or *Bos indicus*, to the American buffalo, *Bison bison*).

Grading—Mating of purebred males of a given breed to non-purebred females and the resultant female offspring in successive generations.

Inbred line—Line of animals produced by mating related animals.

Inbreeding—Mating of animals more closely related to each other than the average relationship within the breed or population concerned.

Incross—Progeny resulting from the mating of animals from different inbred lines within a breed.

Incrossbred—Progeny resulting from the mating of animals from inbred lines of different breeds.

Linebreeding—Generally mild form of inbreeding in which animals mated are related to some supposedly outstanding individual.

Outbreeding—Mating of animals less closely related to each

other than the average relationship within the breed or population concerned.

Outcross—Progeny resulting from the mating of unrelated animals within a breed.

Species cross—Mating of animals belonging to different species (e.g., mating of European breed cattle, *Bos taurus*, to Brahman cattle, *Bos indicus*).

Three-breed rotational cross—A continuous program of cross-breeding in which males of three breeds are used on a rotational basis. Using three breeds designated as P_1, P_2 and P_3, the first generation would involve production of two-breed cross animals, $P_1 \times P_2$. In the second generation, two-breed cross females would be mated to males of the third breed, $(P_1 \times P_2) \times P_3$; three-breed cross females would be mated to males of one of the breeds used to produce the two-breed cross animals, $[(P_1 \times P_2) \times P_3] \times P_1$, etc.

Topcross—Progeny resulting from the mating of animals belonging to different families within a breed.

Topcrossbred—Progeny resulting from the mating of inbred males to non-inbred females of another breed.

Topincross—Progeny resulting from the mating of inbred males to non-inbred females of the same breed.

Two-breed cross—Progeny resulting from the mating of males of one breed to females of another breed.

References

1. Dickerson, G. E., C. T. Blunn, A. B. Chapman, R. M. Kottman, J. L. Krider, E. J. Warwick, and J. A. Whatley. 1954. Evaluation of selection in developing inbred lines of swine. No. Cent. Reg. Publ. No. 38, Mo. Res. Bul. 551.