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Simplified principles for breeding sheep

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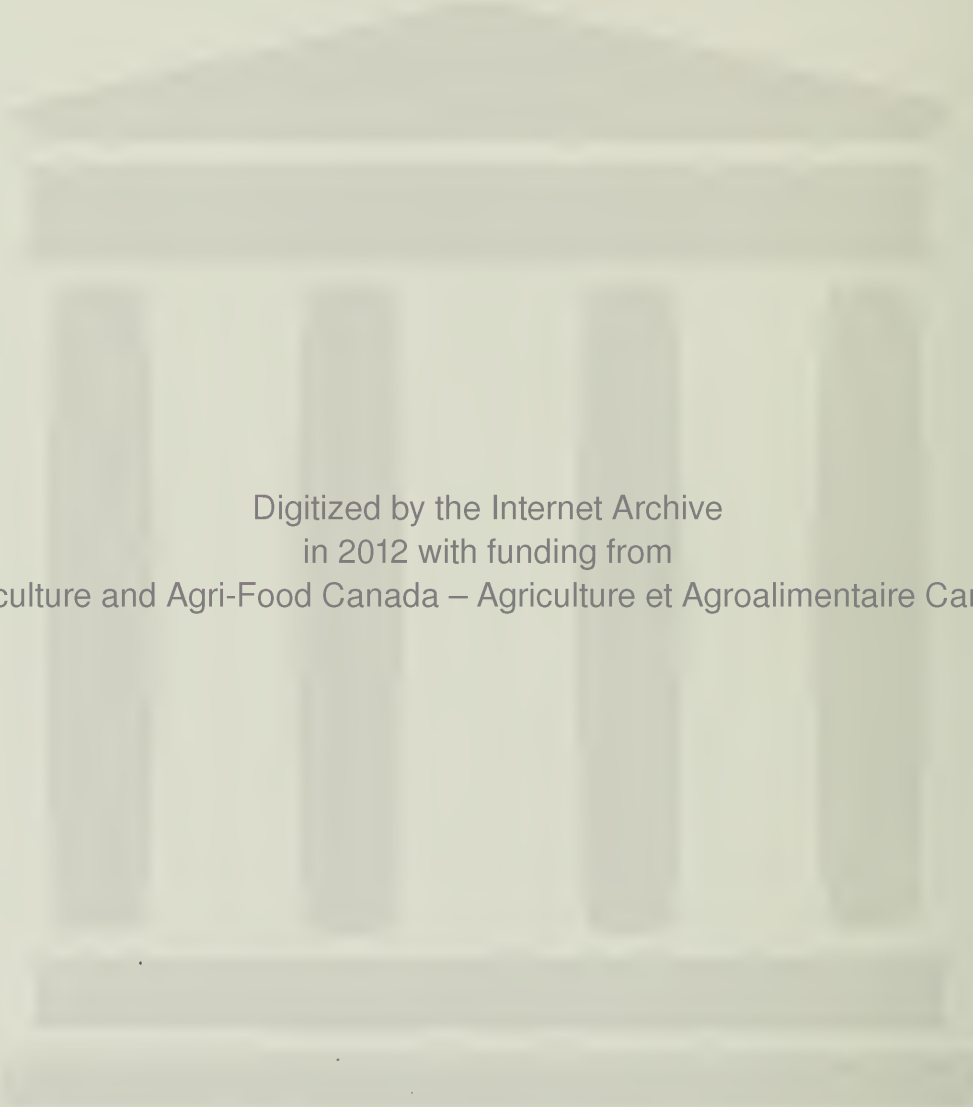
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Preface

This booklet presents some principles of animal breeding to sheep breeders in simple language, so that readers with limited knowledge of genetics and statistics can easily understand and apply these principles. Although the booklet was written with sheep breeders in mind, the principles also apply to other livestock. Familiarizing breeders with existing possibilities and options will enable them to improve the productivity of their animals and maximize their profits.

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Introduction

Animal breeding can be defined as the deliberate and planned alteration of the characteristics of a group of animals so that they can fulfil the demands of the consumer, cope with environment, or respond to different production systems. For example, if the demand is for leaner meat, a breed such as Suffolk or Texel may be considered in a crossbreeding scheme, whereas, if fine wool is in great demand, Merino and Rambouillet sheep may be considered. Also, if the environment is hot and dry, or accelerated lambing is the breeding system used, animal breeding techniques are applied to develop animals well suited for these conditions. Because the force of *natural selection* (selection made by nature to adapt to changing environment) is always at work, the creative involvement of the breeder is to enhance or oppose that natural selection.

Three basic ways to make changes are by *selection*, *inbreeding*, and *crossbreeding*. Advances in molecular genetics have led to new and fast methods for inducing changes by directly manipulating the genetic make-up, such as producing transgenic animals (animals containing genetic material from other organisms). This booklet covers the traditional, basic methods.

Selection

Selection is the force that has induced changes in all creatures from the beginning of creation until now. How present-day animals will evolve in the future depends on the kind of selection done by the breeder and by nature. If breeders practice no selection, nature may do it for them, but they cannot predict the outcome. Natural selection is responsible for many of the characteristics of present-day animals. Even after humans have selected for a specific objective, if their effort is not maintained, nature usually reverts the change achieved back to its previous state.

Breeders practice a kind of selection based on the animal's appearance. A breeder who eliminates animals with under- or over-shot jaws, twisted legs, colored spots, and some other traits considered as faults in certain breeds, despite their merit as breeding animals, selects against defects. These defects may be associated with recessive genes, and the breeder gradually eliminates these genes from the flock. Many breeders also practice selection based on visual assessment of easily measurable traits such as size and fiber quality.

Several factors determine the success and effectiveness of a selection program. The first is to know if the character to be selected for responds to selection or not and to what degree. Selection for a character controlled by one or a few genes (called qualitative or Mendelian traits, because they are inherited according to the simple

laws of Mendel) is very effective. Continuous selection of rams without horns noticeably reduces the number of horned animals and, if selection is also applied on females, the breeder may end with a hornless flock. The same thing happens when selection is made for color, or soundness of teeth.

Most economically important traits in livestock are quantitative traits controlled by numerous genes, each contributing a small effect. Improvement as a result of selection is rather slow. In quantitative traits, the genetic component of the trait is important. To explain that, consider the trait a breeder can measure, as the result of two components: its genetic make-up and the effect of environment. The genetic make-up, i.e., the genes inherited, is fixed at conception and is derived from the two parents. The environment affects the degree of expression of this genetic make-up. For example, if the genetic potential of weaning weight is 20 kg, the lamb that receives ample milk from the dam and enough creep feed to maximize growth can attain that or close to that weight. On the other hand, if the same animal receives less than adequate feeding, suffers from diseases, or any other factor affects its growth, the weight would definitely be less than the 20 kg predetermined by genetics. So environment, whether in the form of nutrition (quantity and quality of feed), management (different types of stress or lack of it), or climate (extreme heat, cold, dampness, or dryness), profoundly affects the degree of expression of the trait, and accordingly the ability to make the right selection decisions.

The environment plays such a great role that in some quantitative traits it may hide the potential predetermined by the genetic make-up of the individual. Traits of reproduction such as fertility, litter size, and lamb mortality are examples of such traits. On the other hand, performance in traits such as wool and mohair production, fiber characteristics, and carcass traits is almost equally determined by the genetic make-up and the environmental effects. Growth traits fall between these two categories.

A measurement for evaluating the genetic component of each trait is called *heritability*. It measures the proportion of the genetic component of the total variation observed. If heritability is zero for a trait, the breeder will lose time and effort trying to select for it. The higher the heritability, the more effective and fast the response to selection would be. The general idea behind heritability estimates is to determine the amount of variation existing between relatives, such as sibs and parent-offspring, as a ratio of the total variation existing between animals of that population. Therefore, heritability may change from breed to breed and even from flock to flock within the same breed. Ideally breeders should calculate the heritability of the traits of interest from the animals of their own flocks. But, since calculating heritability is complicated and requires a large number of animals, use of average estimates from the literature of studies conducted in the past provides the second-best alternative. Breeders can use the average estimates (Table 1) for some of the economically important traits often considered in selection programs.

Table 1 Estimates of heritability from the literature (percent genetic to total variation)

Trait	Heritability estimates	Trait	Heritability estimates
Fertility	3	Lamb survival	10
Prolificacy	14	Grease fleece weight	58
Date of first heat	42	Clean fleece weight	56
Date of lambing	18	Staple length	53
Age at first lambing	31	Resistance to cold	70
Birth weight	28	Total milk yield	53
Weaning weight	20	Ewe productivity	27
Yearling weight	46	Kidney fat percent	53
Mature weight	53	Dressing percentage	25
Lambing interval	6	Carcass lean percent	35

The other important factor is the *variation*. If all lambs weigh 20 kg at weaning, it is impossible to choose parents that would increase weaning weight. So before we can induce change there must be variation, because selection simply means that breeders choose the best parents for specific traits to produce the next generations.

To illustrate the concept and measurements of variation, Table 2 presents an example for corrected weaning weight of lambs in three flocks. The use of the word “corrected” is intentional because breeders should, before practicing selection, correct the records to a standard basis. For example, they should adjust for the influence of factors such as age of dam, type of birth, type of rearing, season of birth, and age at weaning, which among others have significant effects on weaning weight of a lamb. Procedures for correcting records vary in complexity. The simplest procedure is to get the averages for the different levels within the factors, for example, for males and females or singles and twins; then calculate the difference and adjust female and twin records to male and single equivalent by adding the difference to each record. More complex methods consider several factors simultaneously, for example, sex and type of birth of lamb and age of dam all at the same time.

Table 2 Weaning weight of lambs in three hypothetical flocks

Flock	Weaning weight of six lambs for selection (kg)						Mean	Range
	1	2	3	4	5	6		
1	19	19.5	20	20	20.5	21	20	2
2	16	18	19	20	23	24	20	8
3	13	16	19	21	25	26	20	13

Although in the three flocks mean weaning weight of the lambs is 20 kg, the flocks show great differences in variation (see *range* in Table 2). The simplest way to measure variation is to calculate the difference between the smallest and largest measurements. Although the method is simple, its disadvantage is that any extreme value increases the range tremendously. Better measurements, which take into account all the observations, are called *mean deviation* and *standard deviation*. Mean deviation is simply calculated by adding the difference between each observation and the mean (ignoring the sign or otherwise the result would be 0), then dividing by the number of observations. For flock 1, this would be $1 + 1/2 + 0 + 0 + 1/2 + 1 = 3$ divided by 6 = $1/2$, similarly for flock 2 it would be 2.33 and for flock 3, 4. Standard deviation is similar to mean deviation but instead of ignoring the sign, each deviation is squared, all squared deviations added and averaged by dividing the total by the number of animals less one. The next step is to calculate the square root of the average obtained. For flock 1 the standard deviation is $1 + 1/4 + 0 + 0 + 1/4 + 1 = 2\ 1/2$, $2\ 1/2 \div 5 = 0.5$, $\sqrt{0.5} = 0.71$. Both these methods regardless of their complexity show flock 3 to be more variable than flock 2, which in turn is more variable than flock 1.

If the objective is to improve weaning weight in the three flocks by selecting only one male to mate all the females, choose the male with the heaviest weight at weaning, i.e., those weighing 21, 24, and 26 kg in flocks 1, 2, and 3, respectively. Needless to say, the ram in flock 3 will give his progeny more potential for heavier weights than rams chosen in flocks 1 and 2. The difference between the value of the selected ram and the average of all those available for selection is called *selection differential*. In the above-cited example these differentials are 1, 4, and 6 kg, respectively.

In the example, only the best male was selected, in practice the breeder usually needs to select more than one male to avoid inbreeding and in large flocks to service a large number of females. If selection differential is recalculated selecting two males, the selection differential will be lower than when selection was for only one male (because the second best male is inferior). Thus by increasing the number of selected rams, the selection differential decreases, which decreases the selection pressure applied. One important point to remember when calculating selection differential, only consider the animals actually available for selection, because if the best male is already dead, or infertile, there is no point in considering him in the calculations.

To calculate the theoretical outcome of selection assuming again that the average of the flocks is 20 kg, first divide selection differential by 2 because sires contribute only half the genetic make-up of the progeny (the other half comes from the dam). This calculation gives us selection differentials of $1/2$, 2, and 3 kg, respectively. Because the selection applied was based on the phenotype value, which as mentioned earlier is part genetic and part environmental, selection differential should be multiplied by the

genetic portion, i.e., by the heritability. Assuming that heritability of weaning weight is 40%, the genetic gain in weaning weight of the progeny to be expected from selection is 0.2, 0.8, and 1.2 kg in the three flocks, respectively.

If selection is also applied on the females using the same principles, the selection pressure and accordingly selection response may be increased. For example, if half the females in Table 2 are to be replaced, the heaviest will be selected. Thus the selection differential for the females will be 0.5, 2.3, and 4 kg in the three flocks, respectively. Divide each selection differential by 2 and multiply it by 0.4 (as for the males) to arrive at 0.1, 0.46, and 0.8 kg for the three flocks, respectively. So, if selection for weaning weight were applied on both males and females, the genetic improvement expected in progeny of the next generation would be 0.3, 1.25, and 2.0 kg more than the average of their parental generation, assumed in this example to be 20 kg. As a result of many factors, such as inability to obtain accurate measurements or use representative heritability estimates, the observed and expected gain seldom correspond.

In choosing weaning weight as an example, the simplest and easiest scenario was presented, the trait is manifested in both sexes, and the animals are weaned only once in their life. The situation is more complicated when the trait appears in only one sex (such as in selecting for litter size), or the trait requires killing the animals (such as in selecting for carcass traits), or many records exist for each animal (such as in selecting for wool or mohair production).

As a rule, when a character can be measured repeatedly, the breeder can make a more accurate choice as the number of records increases. In most cases, averaging many records decreases environmental variation and may result in higher heritability estimates for the trait. To estimate the *breeding value* (g) (the true hereditary value an animal can transmit to its progeny) of an animal with several records from the flock mean, multiply the deviation of the average of all the records from the flock mean (d) by the heritability (h^2) and then by $[\text{No. records } (n)] \div [1 + (\text{No. records} - 1) \times \text{repeatability } (r)]$, i.e., $g = d \times (h^2 \times n) \div [1 + (n - 1) \times r]$.

Repeatability (r), most simply defined, is the correlation between the different records. In the case of wool production, for example, it is the correlation between first and second fleece weights. Given a third fleece weight, it is the average between the three possible correlations (1 and 2, 1 and 3, and 2 and 3). Repeatabilities are usually higher than heritability and preferably should be calculated for each specific flock. However, many estimates are available in the literature for most of the important traits.

To illustrate the effect of multiple records, assume heritability is 30% and repeatability is 0.6 in a flock with an average of 40. If the selected animal had three records averaging 43, its breeding value is $(3 \times 0.3) \times [3 \div (1 + 2(0.6))] = 1.227$. This value is higher than 0.9 calculated if the animal had only one record of 43 (3×0.3). On the other hand waiting for multiple records to accumulate has the

adverse effect of increasing the *generation interval* and eventually reducing the genetic progress achieved per year.

To illustrate that, if we consider the generation interval to be 2.5 years and assume the genetic gain made to be 0.8 kg, the genetic gain per year is $0.8 \div 2.5 = 0.32$ kg. If by using multiple records we not only increase the genetic progress to 1.0 kg but also increase the generation interval to 3.5 years, the yearly progress is $1.0 \div 3.5 = 0.28$ kg, lesser than in the first case. In the same context, by reducing the generation interval we can increase genetic progress per unit of time. For example, mating ewes at early age to lamb as yearlings results in faster gain per year than delaying their mating until they reach 1 year of age. Also, using Record of Performance programs to predict the breeding value of animals has the same effect.

Selection based on relatives

How can a breeder select for a trait expressed only in one sex, for example, for litter size or milk production? At one time or another, breeders selected their sires from those born twins and triplets and from those born to good mothers. Using this principle, breeders should examine the performance of close relatives that show the trait, and select accordingly. To select males for prolificacy, examine the performance of females over many reproductive cycles, take the average of these performances, and select the sire from the mother that gave the highest performance. The same principle also applies when selecting for traits that require slaughtering the animal, such as carcass quality. One method for selecting for carcass merit is to examine the performance of relatives. For example, the breeder can maintain half and full sibs, send some of them to slaughter, and keep the animals whose sibs demonstrate the highest performance.

Applying another procedure, breeders can obtain progeny from the sires considered for selection and test these progeny for the desired traits. This process, although lengthy and expensive, is considered the most accurate because breeders test what they would eventually get from their selections of particular sires. This *progeny testing* procedure, now widely used in dairy cattle breeding, is responsible for the great improvement obtained. When breeders select based on ancestors, they practice family or pedigree selection, and when they select based on the offspring then they practice progeny testing. Both methods are effective in selecting for traits limited to one sex.

Multiple-trait selection

Often sheep breeders have a wider objective for their animals: they should be prolific, fast growing, and produce heavy fleeces and carcasses with more lean and less fat. Various procedures can help to achieve these objectives.

Tandem selection

In the first method, breeders select for each character one at a time in sequence, which may take a long time to achieve. However, there is no guarantee that by the time breeders complete their selection for the last trait they will not already have lost the gain achieved in the early traits.

The alternative is to select for more than one character at the same time. The problem is that, by increasing the number of traits under selection, we decrease the amount of genetic improvement possible had we selected for each trait separately. Simply, finding animals that excel in *all* selected traits is next to impossible. What can complicate the matter further is the possible genetic correlation between the traits in question.

Genetic and phenotypic correlations are measures of how closely the traits are related to each other. For example, the length of the wool and the weight of the fleece are positively correlated, an increase in one results in an increase in the other. Litter size and lamb birth weight is another example. The two traits are correlated but inversely; so an increase in litter size results in a lighter lambs at birth. These two examples illustrate a positive and a negative correlation. As shown in the first section, the expression of each trait results partly from genetics and partly from environment; the combined effect, called phenotype, is what one can measure. Correlation based on the direct phenotypic measurement taken, such as litter size or lamb weight, is called *phenotypic correlation*.

Genetic correlation is based on the genetic part only and is the one important in selection. If it is positive, a strong correlation implies that the same genes are working in the breeder's favor improving both traits. However, if it is negative it implies that improving one trait causes the other one to deteriorate. Genetic correlations result from genes affecting more than one trait, from genes being so closely linked to each other that they mostly transmit as one block, or from different genes interacting together, or all three. Certain traits may not be correlated at all.

The following methods are used to select for more than one trait simultaneously.

Independent culling levels

In this method the breeder sets a standard for each trait for selection and chooses animals that satisfy these levels. The breeder culls any animal below these levels for any one trait regardless of its performance in other selected traits. This simple method has its drawbacks. It does not take into account the relation between traits and fails to capitalize on animals superior in one trait but intermediate in others. Also it gives no economic consideration to the different traits selected, even though one trait can be more important than another.

Selection indices

Constructing and using *selection indices* is the most efficient way of selecting for more than one trait, especially when correlation between traits is low or negative. This method takes into account all the drawbacks mentioned earlier. According to Dr Hazel, who suggested this method: “give each animal a true value by adding into one figure the credits and penalties given each animal according to the degree of its superiority or inferiority in each trait.” The idea is simple, each trait is expressed as a deviation from the mean for all animals in the flock. However, the problem with this method is the complexity of calculating it.

First weigh each trait by its standard deviation and combine them all in one figure. This step standardizes traits measured in different units and avoids having to add lambs to kilograms to centimetres. Then weigh each trait by its economic value. Breeders selecting for litter size and wool production, for example, should find out how much a lamb and a kilogram of wool are worth, and the relative value of one to the other. Heritabilities and phenotypic and genetic correlations among the traits are required to calculate selection indices. These calculations are complicated and requires the use of computers. The index is a set of figures for each trait. For example, the following index was calculated for live weight (LW), grease fleece weight (GFW), and fiber diameter (FD):

$$\text{Index} = 200 - 1.32 \text{ LW} + 30.73 \text{ GFW} - 7.197 \text{ FD}$$

Multiply the actual values for the performance with these figures and add them all together. The end result is one figure for each animal.

In some indices, instead of the actual values, the deviations from the flock means are used instead, in such cases the breeder calculates the deviation of each trait from flock mean and uses these deviations to calculate each animal's index. After ranking the animals in descending order, the breeder selects the highest animal in the list.

Breeders who do not want such sophistication and who know that the traits they want to select for are positively correlated can construct a simple index themselves. All they need to know is the standard deviation of the traits in question, which can be calculated from the records as outlined before, and their relative economic value.

Obtain the relative economic value by dividing the returns of the traits. For example if a unit of wool production (1 kg of grease fleece weight) is worth 4 dollars, a unit of weaned lamb (1 kg of weaned lamb) is worth 2 dollars and the unit of prolificacy (1 extra lamb weaned) is worth 32 dollars, the relative value of the three traits is 1 : 1/2 : 8, respectively. Then divide the performance of each animal for trait one by its standard deviation and multiply the result by the

relative economic value of that trait. Repeat that for each trait under consideration and, by adding all these figures, arrive at one estimate for each animal. Then rank the animals according to the calculated estimates and select those on top for reproduction.

Choosing effective selection plans

Before determining which selection plan to choose, consider the following:

- What is the overall objective of the improvement? What are the traits to consider, taking into account their relative importance and economic values?
- How precisely will these traits be measured and recorded?
- What are the variation, repeatabilities, and heritabilities of each trait, and the phenotypic and genetic correlations among these traits?
- What procedure will be followed to correct for environmental differences, such as sex, type of age, and age of dam?

Based on this information, choose the appropriate selection procedure according to the following guidelines:

- If heritability is near 0.3 or higher, select on the individual's own record; it indicates enough of the animal's breeding value.
- If repeatability is high, then one record for each animal is sufficient, and there is no real advantage of waiting for more records, because this would increase the generation interval needlessly and reduce progress.
- If heritability is low (i.e., between 0.1 and 0.25), examine ways of increasing the accuracy of the selection; consider progeny testing.
- If the trait is expressed in one sex or can be measured only after slaughter, examine progeny testing and use of half-sib families.
- According to the number of traits to be considered in the selection program, decide on the appropriate method.

The preceding section can be summarized in the following recommendations:

- 1) Select for heritable characters that respond to selection: identify these by the magnitude of their heritabilities.
- 2) Give animals the optimum feeding and management treatment to express their genetic potential fully; avoid the risk of culling superior animals and selecting instead inferior ones simply because management prohibited the superior animals from showing their real potential.
- 3) Because selection depends on variation, try to increase variation in the flock before embarking on selection; continuous inbreeding and use of closely related rams reduce variability, whereas outbreeding increases it.

- 4) Whenever possible, select for both males and females, so as to increase the response to selection.
- 5) Increase selection pressure by reducing the number of parents selected. In large flocks it may be preferable to consider dividing flocks into different strains, select within these strains, and cross them from time to time to increase variability.

Inbreeding and crossbreeding

Besides selection, breeders can also change the characteristics of the animals they raise through *inbreeding* and *crossbreeding*. Breeding systems applying both or either means combined with selection are also common. In this booklet inbreeding and crossbreeding are presented concurrently, because they represent the same phenomena but in opposite directions.

Because breeds are developed from other breeds, even animals of different breeds can still be related. It is therefore, proper to start by introducing some definitions and concepts.

To avoid inbreeding, breeders are encouraged to introduce new blood or cross their animals with other breeds. Many breeders may not realize that the animals they presently raise were probably developed by intensive inbreeding a few centuries earlier, when breed development and improvement were made based on inbreeding and line crossing.

Animals within a population can be members of the same family or the same flock or come from the same town, county, province, country, and so on. They can be from the same or different breed and species. The closeness of the animals to each other, i.e., their degree of relationship can vary accordingly. Animals from the same family are more closely related than animals from the same flock, which in turn are more closely related than animals in the same town, county, and so on.

Determining the *degree of relationship* between individuals is important because it clarifies whether the mating is inbreeding or crossbreeding. The strongest relationship in the plant kingdom is between the individual and itself, which exists where self-fertilization is possible in certain plants. The closest relationship in the animal kingdom is between identical twins, who possess the same set of genes. The next closest relationships are between full sibs and parent-offspring. Because half the genes between full sibs or between parent and offspring are common, their relationship is $1/2$. By going further away in relationships, the number of common genes starts to decrease; for half sibs, double first cousins, and grandparent-offspring it is $1/4$.

Coefficient of relationship

This coefficient measures the degree of relationship, and the procedure for calculating it is simple. First, redraw the pedigree of the animals as presented in Fig. 1a, connecting the two animals in question through their common ancestors as in Fig. 1b. Next, count the number of lines (paths) connecting the animals through their common ancestors, making sure not to repeat any path twice.

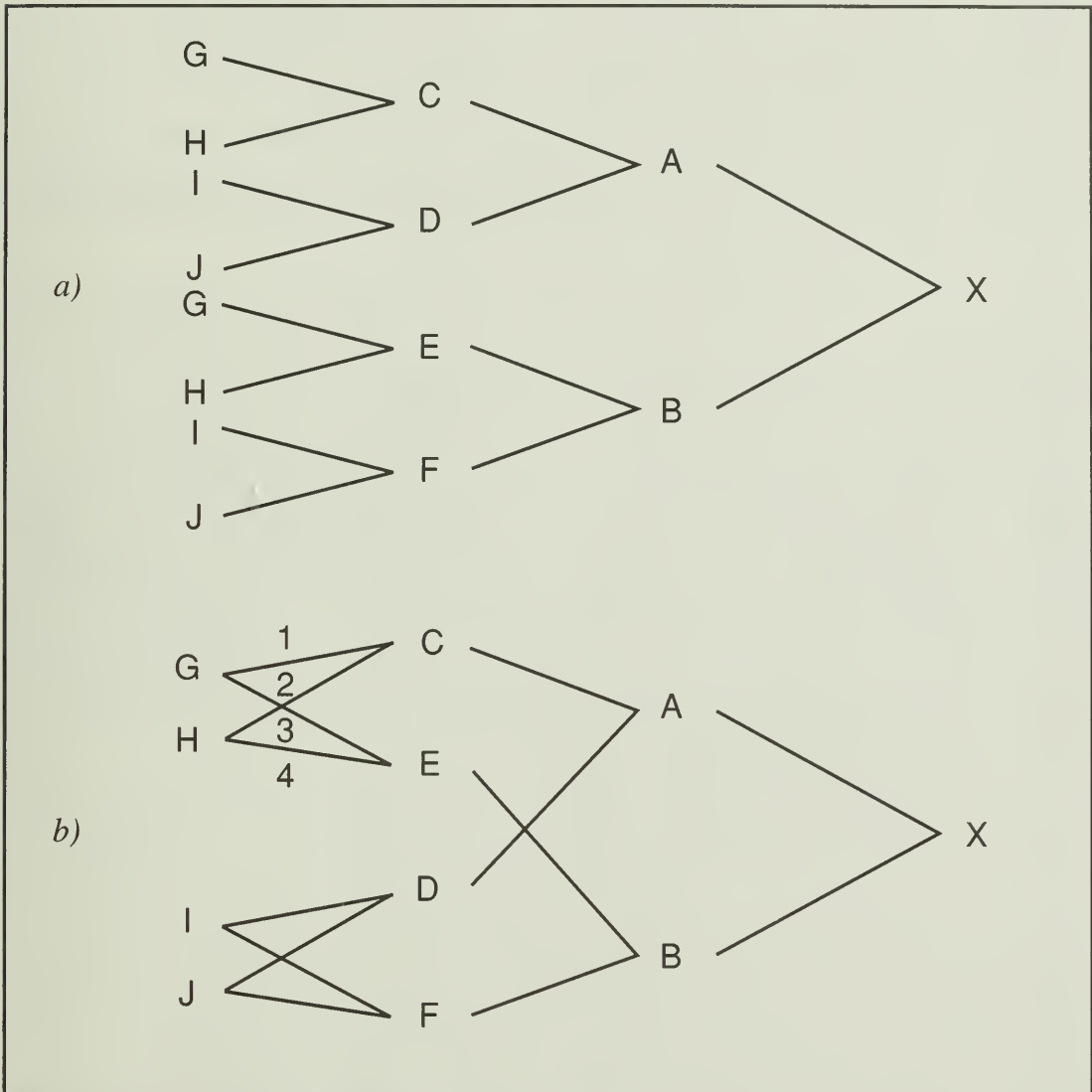


Fig. 1 a) The pedigree of animal X; b) Modified pedigree of animal X.

For example, C and E are connected through the parent G (two lines, 1 and 2) and the parent H (two lines, 3 and 4); likewise the animals D and F. Then, multiply $1/2$ by itself the number of times equivalent to the number of connecting lines for each common ancestor separately. For C and E, it is $1/2 \times 1/2$ through G and $1/2 \times 1/2$ through H. Finally, add all possible calculations, the relationship between the full sibs C and E or D and F is $1/4 + 1/4 = 1/2$. The

relationship between A and B is four 4-line connections: ACGEB, ACHEB, ADIFB, and ADJFB. The relationship is then

$$(1/2 \times 1/2 \times 1/2 \times 1/2) + (1/2 \times 1/2 \times 1/2 \times 1/2) + (1/2 \times 1/2 \times 1/2 \times 1/2) + (1/2 \times 1/2 \times 1/2 \times 1/2) = 1/16 + 1/16 + 1/16 + 1/16 = 4/16 \text{ or } 1/4,$$

which is the relationship between double first cousins.

The relationship can be calculated between any two animals regardless of generation, for example, between B and C, BEGC and BEHC (three paths each), $1/8 + 1/8 = 1/4$. In both cases the $1/4$ implies that 25% of the genes in the two animals considered are identical due to sharing common ancestors. The mathematical expression to calculate inbreeding coefficient is $\sum(1/2)^{n+n'}$ where \sum means the summation, n is the number of paths between the individual 1 and the common parent, and n' is the number of paths between individual 2 and the same parent. For example, the coefficient of relationship between C and E is

$$1/2^{1+1} + 1/2^{1+1} = 1/4 + 1/4 = 1/2.$$

Homozygosity and heterozygosity

Each animal cell contains a nucleus in which chromosomes are present. On each chromosome genes are arranged in specific locations called the *locus*. Except in reproductive cells, i.e., male sperms and female eggs, where only one of each chromosome is present, in all other cells each locus has one copy of the gene coming from the father and the other copy coming from the mother. If both are similar (● and ● or ○ and ○), the animal is called *homozygous* for that locus. When the two copies are different (● and ○), the animal is *heterozygous* for that locus.

The genes present in each cell are responsible for the inheritance of characters. The simplest example is when the character is controlled by one gene, for example, having or not having horns. If the solid dot (—●—) represents having horns, a hollow dot (—○—) represents pollness (hornless), in genetic terms, each of the two alternatives is called an *allele*. Each animal should have two copies of the same gene, one coming from each parent. If both are solid (—●—, —●—), then the animal is horned; if both are hollow (—○—, —○—), then the animal is polled. Geneticists call this situation *homozygous* for that trait. The animal can also have one hollow and one solid allele (—○—, —●—) and is then called *heterozygous* for that locus. Its performance then depends on the reaction of the two alleles, i.e., does one allele override the other and mask its effect (dominant) or do both contribute to performance, in which case the heterozygote differs from both homozygotes.

To illustrate the effect of mating system on the degree of heterozygosity, consider the three cases presented in Fig. 2. In (a) many of the loci have similar alleles, whether solid or hollow, in (b) many of the loci have different alleles, while in (c) the number of the

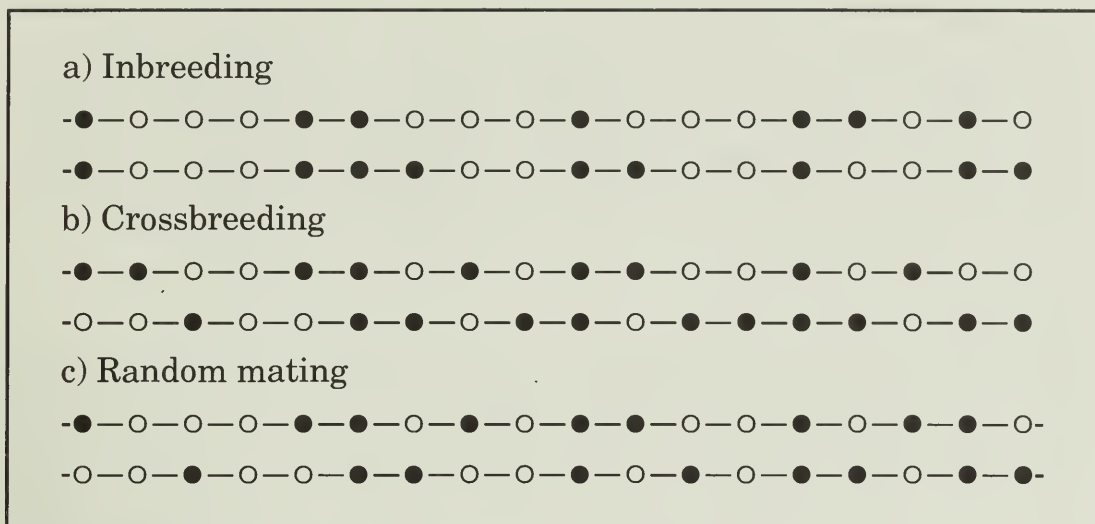


Fig. 2 Effect of mating plan on homozygosity.

two alleles is balanced. If (c) represents the average animal, then inbreeding has the effect of changing them to (a) and crossbreeding to (b). This example illustrates increase in homozygosity (a) and increase in heterozygosity (b).

The effect of inbreeding is to increase homozygosity. When mating closely related animals, there are greater chances that the alleles from both parents are similar because of common ancestors, and the alleles get together in the offspring. The outcome depends on what these alleles do. If they increase production, then inbreeding could be beneficial, but if they have adverse or lethal effects then inbreeding is undesirable.

Dominance plays a role in this regard. Each individual can carry the undesirable allele, but its effect is masked or covered by the other dominant allele. By mating two carriers of the undesirable allele, there is one chance in four that the individual will show the undesirable effect (Table 3). In humans, albino babies born to normal parents are an example of this phenomena.

If inbreeding tends to increase homozygosity, the effect of crossbreeding is the opposite, it reduces homozygosity and increases heterozygosity. The change in homozygosity is associated with two opposite phenomena, *inbreeding depression* and *heterosis*. It is well recognized that the effect of inbreeding is most evident in traits related to fitness, such as survival, fertility, and prolificacy and less evident in traits related to production, such as wool and carcass quality.

Table 3 Possible progeny of mating two carrier parents

Parents (carriers)	A	a
A	AA (noncarrier)	aA (carrier)
a	Aa (carrier)	aa(undesirable effect)

Inbreeding coefficient

This coefficient measures inbreeding and is usually referred to by the letter F. It is defined as the probability that the two copies of a gene present at any loci are inherited from the same ancestors that the parents have in common. It is thus a measure of the common ancestry of the two parents. To estimate the inbreeding coefficient of an individual, draw its pedigree and follow the common ancestors over the generations as shown earlier.

To calculate the inbreeding coefficient, breeders should examine the pedigree of the animal as far back as they can. If the ancestors are not themselves inbred, the coefficient can be calculated by multiplying the coefficient of relationship between the two parents by $1/2$. In the next pedigree (Fig. 3), if the animal X did not have the animal G in its pedigree, its inbreeding coefficient would have been derived directly from the coefficient of relationship between its parents (A and B), $1/2 \times 1/2 = 1/4$ or 25%. As a result of the common ancestor G the percentage would increase because the parents were inbred. In the example, the parents A and B are related through the common ancestors C, D, and G. The relationship of AB through C (ACB) is $1/2 \times 1/2 = 1/4$, through D (ADB) is $1/2 \times 1/2 = 1/4$, and through G, two paths, (ACGDB) $1/2 \times 1/2 \times 1/2 \times 1/2 = 1/16$ plus (ADGCB) $1/2 \times 1/2 \times 1/2 \times 1/2 = 1/16$, or $2/16$. The sum of all paths is thus $1/4 + 1/4 + 2/16 = 5/8$. The coefficient of relationship between A and B should be corrected for their own inbreeding by dividing by the square root of $1 + F$ for A multiplied by the square root of $1 + F$ for B, i.e., square root of $(1 + 1/8) \times (1 + 1/8)$. The final calculation for coefficient of relationship between A and B is $5/8$ divided by $9/8 = 5/9$ and the inbreeding coefficient for X is $1/2 \times 5/9 = 27.8\%$. The contribution of the grandparent G in this example was the 2.8% difference between 27.8 and 25% if C and D were not related.

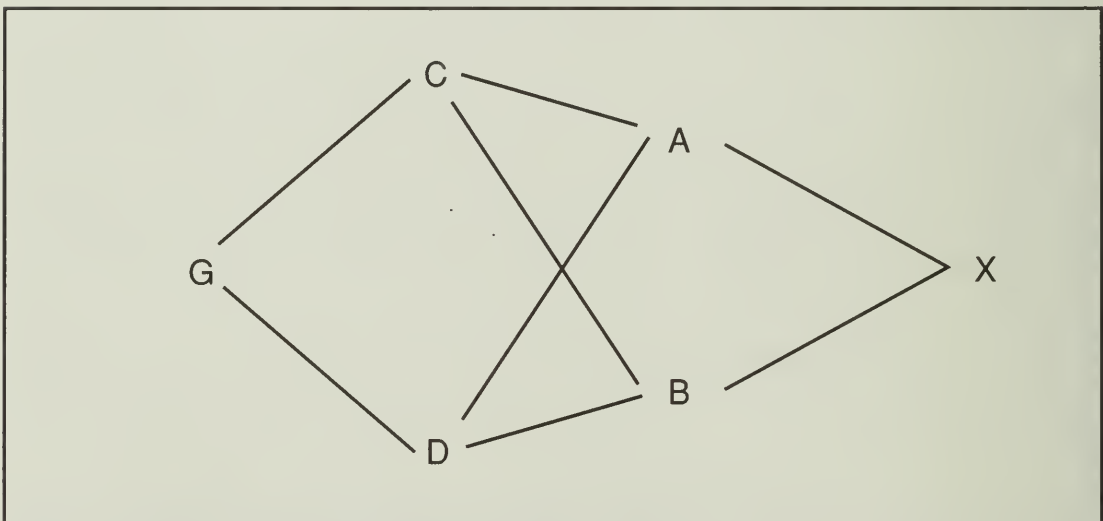


Fig. 3 Pedigree of animal X from inbred parents.

The inbreeding coefficient ranges from 0 to 100%. In a large population of animals under random mating, the coefficient will be close to zero. However, under nonrandom mating, or when the number of animals is small, the coefficient will increase up to 100% achieved when the animals mated have the same set of genes coming from common ancestors.

Classification

Ruminants are classified into four families, one of which is Bovidae, which is subdivided into two subfamilies, Caprinae and Bovinae. Within Caprinae, sheep and goats belong to two different genera. Cattle, buffalo, and bison belong to three different genera within the Bovinae subfamily.

Breeds

A breed can be defined as a population of animals with distinct characteristics that differ from those of other populations within the same species. The traits that characterize a breed can be related to appearance, e.g., hair type, hair color, and horns, or to production and reproduction, such as size, prolificacy, precocity of sexual maturity, length of the breeding season, wool, and milk yield. For example, a breed such as the Suffolk differs in many of these aspects from Dorset and from Romanov. However, production traits show continuous variation and no clear dividing line can be drawn between breeds, even when the breed averages differ rather widely from each other. Thus, Suffolk is considered a nonprolific breed, yet some ewes produce triplets and quadruplets, whereas ewes from the prolific Romanov breed may produce singles. Important production traits, such as growth and wool production, are influenced by a large number of genes (called quantitative traits to distinguish them from traits such as presence of horns, controlled by one or a few genes and called qualitative traits). A considerable degree of heterozygosity exists within all breeds with regard to all quantitative traits.

As used in practice, the term *pure breed* refers to animals that are registered, or eligible for registration, in a herd book. These “purebred” animals constitute a selected group, intended for use in breeding. The requirements for an animal’s acceptance in a herd book vary with time and place. The breed concept in practical breeding is conventional. The division into breeds is justified, however, because populations constituting the breeds have been specialized for different purposes and for differing local conditions.

Breeding within the same breed has been called *pure breeding* and matings between animals of different breeds or lines has been called *crossing*. The term *crossing* is used here in a wider sense, for example, *line crossing* describes mating between strains or lines within the same breed. Crosses between different breeds are referred

to as *breed crossing*. Often a breed can be divided into different *strains*, either when, from a breeding point of view, they are more or less isolated from each other due to geographic conditions, or when, in some respects, the aim of breeding is different.

Lines

A line indicates a collection of animals, which, as a result of inbreeding, are more closely related to each other than to the other individuals in the strain or breed. If an inbreeding coefficient of at least 0.375, corresponding to two generations of full-sib mating, is reached, then such a line is called an *inbred line*. *Family* is used to indicate full or half sibs. Consequently, all individuals within a family are equally closely related to each other.

Heterosis

Heterosis measures the superiority observed in the progeny born to parents of different genetic backgrounds, whether lines, strains, breeds, or species as compared to the average of the two parents involved. There are different types of heterosis: individual, maternal, and paternal.

Individual heterosis

Individual heterosis (H_I) is that observed in the animal itself, because it is a cross. The ideal method for estimating individual heterosis is to produce reciprocal crosses from mating say breed A rams with breed B females and breed B rams with breed A females. At the same time, mate breed A and breed B males to females of their respective breeds. The results are AA, BB, AB, and BA groups. Raise the animals of the four groups under similar conditions and evaluate their performance. Individual heterosis can be calculated as follows:

$$H_I = 50 \times [(AB + BA) - (A + B)] / (A + B)$$

For example, if average weaning weights of breeds A and B are 20 and 24 kg, respectively, and those of AB and BA crosses are 26 and 29 kg, respectively, the individual heterosis of weaning weight will be $(26 + 29) - (20 + 24) = 11$, divided by $(20 + 24)$ and multiplied by $50 = 12.5\%$. This ideal unbiased estimate takes into consideration the possible difference in *maternal ability* of breeds A and B. For example, if breed A ewes produce more milk than breed B females, then the progeny BA grow faster than the progeny AB, even though they are similar genetically. By taking the reciprocal crosses this maternal ability is accounted for. However, breeders would seldom make the reciprocals simply because most of the time they use only sires from different breeds on their female population. The ratio

$$S_I = 100 \times [AB \text{ (or BA)} - (1/2A + 1/2B)] / (1/2A + 1/2B)$$

measures the superiority (S) of a combination over the parental breeds. Although this measurement should not be referred to as heterosis (because only one cross and not the two reciprocal crosses was used in the calculation), it is still a valid measurement of how the cross performs compared to the average of the two parents.

In most cases the ewes are crossed with rams from superior breeds, so another measure of superiority is to compare the cross to the better parent breed, for example AB vs B, if B happens to be the better parent.

Maternal heterosis

Maternal heterosis is defined as the extra advantage a lamb receives from its crossbred dam in the form of higher milking and mothering ability as compared to purebred dam. Maternal ability of the dam is calculated from two sources of crossbreeding programs.

First, when crossbred and purebred parental breeds are available at the same time and mated as follows:

- all with rams of a third breed (C)
- all with rams of a genotype with 50% of genes from each of the parental breeds (F₁ or F₂)
- half of each female group with rams of breed A and half with rams of breed B.

The reason for the restriction on the sire is to avoid confounding the individual with the maternal heterosis. The calculating equation for maternal heterosis is

$$H_m = 50 \times [(C \times AB) + (C \times BA) - (C \times A) + (C \times B)] / [(C \times A) + (C \times B)].$$

Second, maternal heterosis can also be calculated from crossbreeding experiments involving F₁ and F₂ females. Estimates using this method are often less accurate because of selection or inbreeding, or both, when generating F₂ animals. This comparison estimates only half the heterosis so multiply the figure by 2 to get the actual heterosis.

Paternal heterosis

Paternal heterosis is the advantage of the crossbred over a purebred sire. It is manifested in traits such as libido, sperm production, and quality. To evaluate paternal heterosis, expose sires from the two purebreds and crossbreds to dams from preferably a different breed. Then take measurements (sperm production, quality) or observations (number of mountings within a specific time). Use the same equation as that used for estimating individual heterosis to estimate paternal heterosis.

Mating systems

The aim of a particular mating system can be either to increase or decrease the homozygosity of the progeny, compared with the parents, or in some cases to maintain the degree of homozygosity unchanged. This aim constitutes the basis of the following classification.

Random mating

Under random mating, which is not necessarily unplanned, any sire has an equal chance of mating any dam. Random mating can still be planned if the objective is to keep unchanged the genetic composition of the population and the degree of heterozygosity. Because continuous improvement is always an important objective, no commercial breeder would deliberately put his animals under random mating. However, in selection and other genetic studies, a *control population* maintained by random mating is needed for evaluating response to selection.

Breeding for increased homozygosity

Often, but not always, breeding for increased homozygosity means breeding within a breed. *Inbreeding* can be defined as mating between animals that are more closely related to each other than the average relationship between all individuals in the population, for example a breed. Breeding within small populations leads to an increase in inbreeding. In practical terms, mating between animals that are less closely related than cousins has so little effect on the degree of inbreeding that it may be ignored. Matings between half-cousins only slightly increases the coefficient of inbreeding.

Inbreeding can be either occasional or consistently carried out for several generations. Three main types of consistent inbreeding systems can be identified.

Close inbreeding

Close inbreeding uses matings between sibs or between parents and progeny to achieve inbred lines with a relatively high degree of homozygosity. One of the methods most often used is full-sib mating for many generations. The same effect can be achieved by consistently backcrossing the progeny to the younger of the parents. Half-sib mating is much slower in reaching homozygosity but is also less risky. By applying less-consistent and milder inbreeding, the same results may be achieved but over a longer time.

Strain formation

Strain formation is a considerably milder form of inbreeding. In the long run it leads to increased homozygosity within the strains.

Linebreeding

Linebreeding is inbreeding to a superior parent (Fig. 4) within an ancestral line to increase a particular male or female ancestor's proportion of the genetic constitution of the progeny. The most intensive form of linebreeding is backcrossing to the same parent for several generations in succession. Usually, a much milder form of linebreeding is employed, such as mating a female with a grandsire, or an uncle who carries half of the grandsires genes.

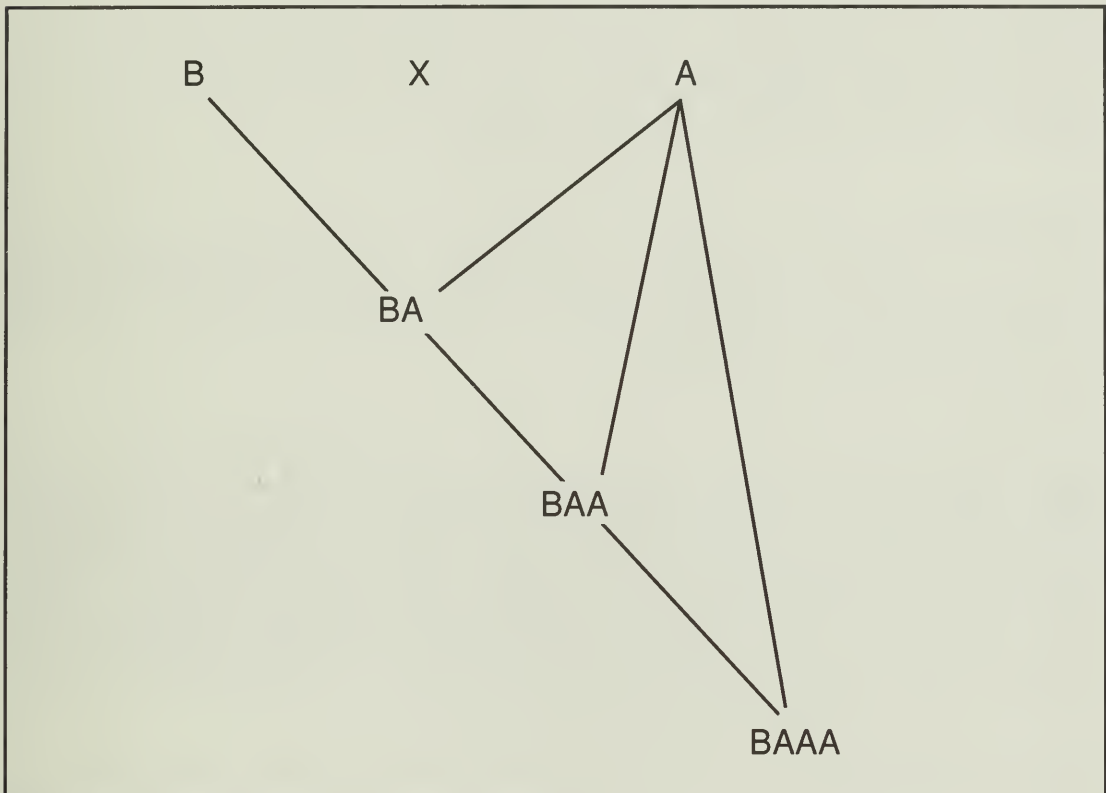


Fig. 4 Line breeding to superior parent A.

Mating based on phenotypic resemblance

This system of mating pays no regard to degree of relationship; the mating combinations are selected only according to the external resemblance of the animals; the mating is of "like with like." In inbreeding, identical genes are brought together regardless of their effect; but when mating is on the basis of external resemblance, genes having a similar effect are brought together, regardless of whether they have a common origin or not. Consequently, this system of breeding has less influence on the degree of homozygosity than inbreeding. The method of mating "like with like" can effectively contribute to the differentiation of the breeding material when the heritability is high for the traits in question. However, the effectiveness declines with lower heritabilities. It is also possible to

mate “unlike with unlike” and produce an intermediate form, but this leads to an increase in heterozygosity. In practical animal breeding, breeders pay attention both to relationship and to external resemblance in selecting mating combinations.

Breeding for increased heterozygosity

Outbreeding

Outbreeding, the opposite of inbreeding, is done within a pure breed. The relationship of the animals mated is less close than the average relationship within the population (breeders’ flocks for example). Breeders practice this type of mating when they buy rams from other breeders. Mating between inbred lines or strains within the same breed is also a form of outbreeding.

Crossing

The following mating systems, although usually used for crossing different breeds, can also be used for crossing inbred lines or different strains within the same breed.

Single two-way crosses

Two different populations A and B, which can be breeds, inbred lines, or strains, are crossed with each other to produce a first-cross (F_{AB}) generation. The F_{AB} individuals exhibit maximum individual heterosis and are used only for market purposes. The disadvantage of this method is the need to maintain a relatively large number of the parental types to continue the crossing in closed flocks, or the continuous need to buy sires for breeding.

Three-way crosses

The first-generation crossbred females (F_{AB}), produced from single two-way crosses as above, are crossed with males of a third line, strain, or breed (C), to produce three-way crossbred animals (Fig. 5). They are usually slaughtered for market. This method capitalizes on the full potential of maternal and individual heterosis. It uses crossbred females and capitalizes on maternal heterosis in traits related to reproduction, survival, and fitness. Individual heterosis is expressed in growth and carcass quality traits in the three-way cross progeny. A second method for three-way crosses is to mate crossbred rams to purebred ewes, capitalizing on the hybrid vigor of the crossbred rams in libido and sperm production. A third procedure, seldom used in practice, is to cross first-cross parents having one type in common, for example, $M_{AB} \times F_{AC}$. The progeny benefit from paternal and maternal heterosis, and to a lesser extent from individual heterosis.

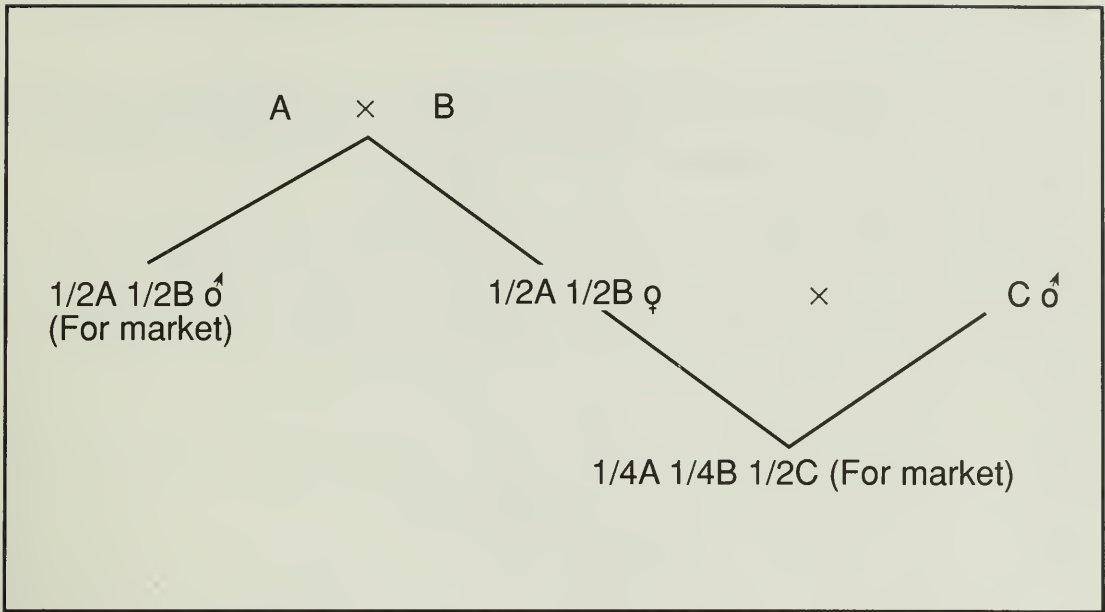


Fig. 5 Three-way cross.

Four-way or double crosses

Populations A and B are first crossed with each other, as are C and D, to obtain the F_1 generations F_{AB} and F_{CD} . These are then crossed together to give the “double hybrids” $F_{(ABCD)}$ (Fig. 6). This method capitalizes on the full potential of maternal, paternal, and individual heterosis but is difficult to practice on farms.

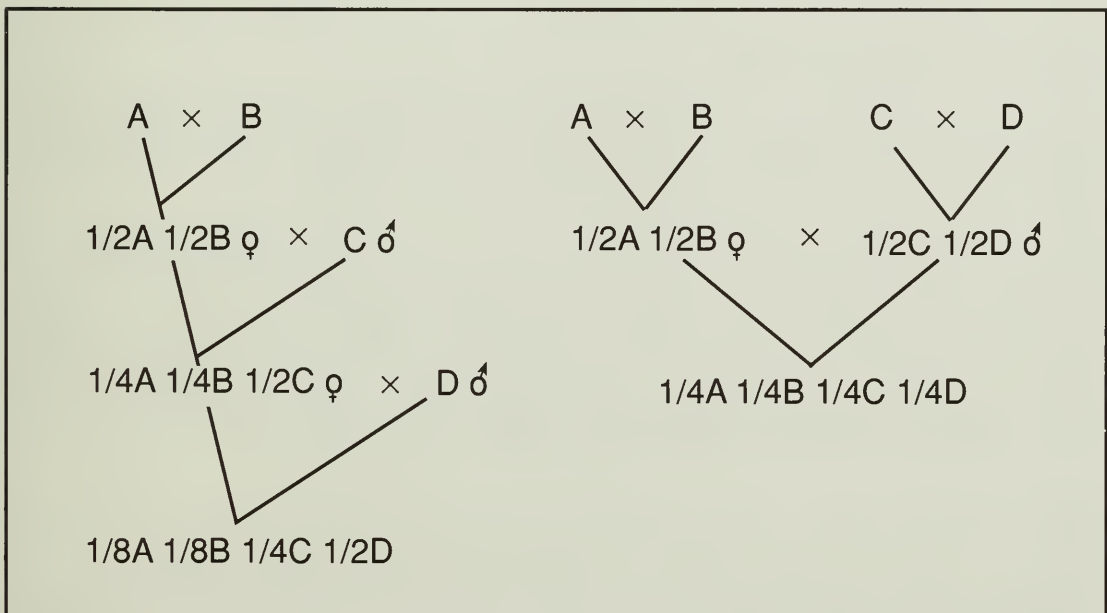


Fig. 6 Two alternative four-way crosses.

Backcrosses

The first-cross females (F_{AB}) are backcrossed to males of one of the parental breeds involved in producing them. The offspring have 75% of the genes from one breed and 25% from the other (Fig. 7) and are usually used for meat.

The advantage of this method is the full use of maternal heterosis, especially when the F_1 females are better mothers than females from either of the parent populations. The disadvantage of the method is the discontinuity and need to keep two separate breeds in the flock.

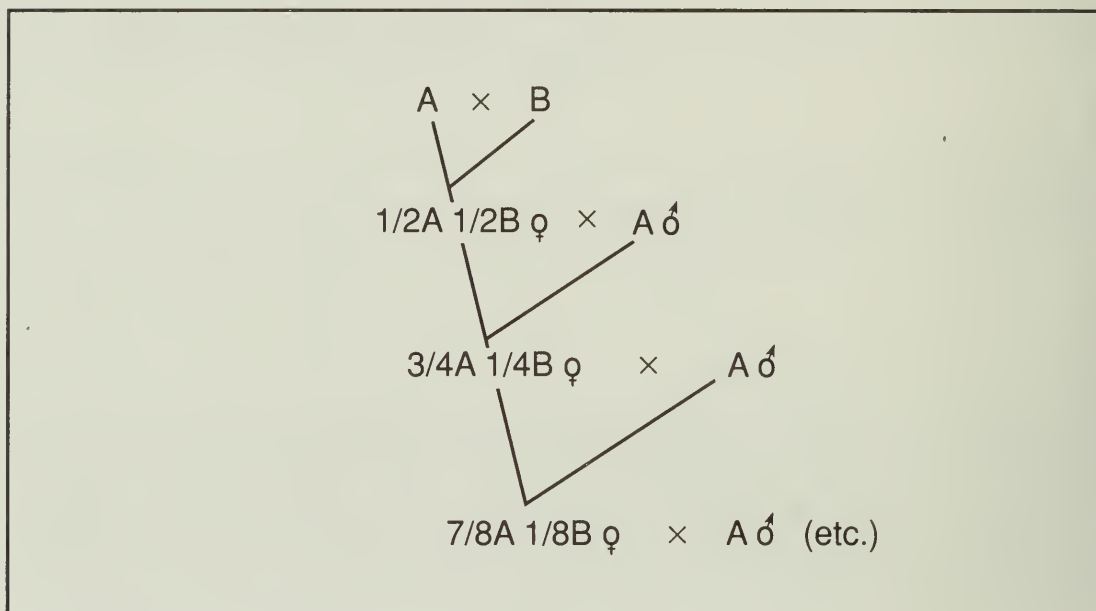


Fig. 7 Backcrossing to breed A.

Rotational crossbreeding

Crossbred females are mated with males from one of the parental breeds, then the breed of sire is alternated for each new generation. Three types of rotational crossbreeding are common.

Criss-crossing (two-breed rotational) Breeds A and B are crossed to produce an F_1 generation, then F_{AB} females are backcrossed to males from breed B, the $F_{(AB,B)}$ females are then mated back to males from breed A, and so on (Fig. 8). The advantage of this method over the two-way cross is that crossbred females can continue to be used for breeding, and only purebred males need be purchased.

Three-breed rotation F_{AB} females are mated with males from a third breed, C. Rams from breed A are used on the next generation of females, rams from breed B on the following generation of females, rams from breed C on the following, and so on.

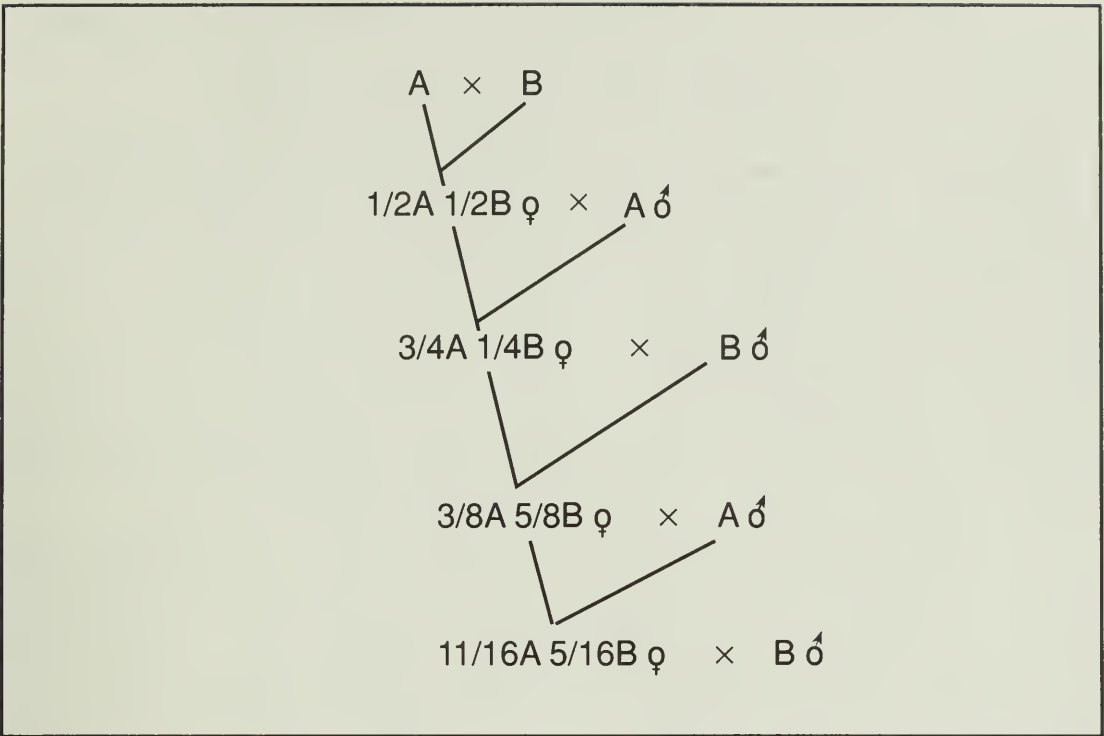


Fig. 8 Two-breed rotational crossing.

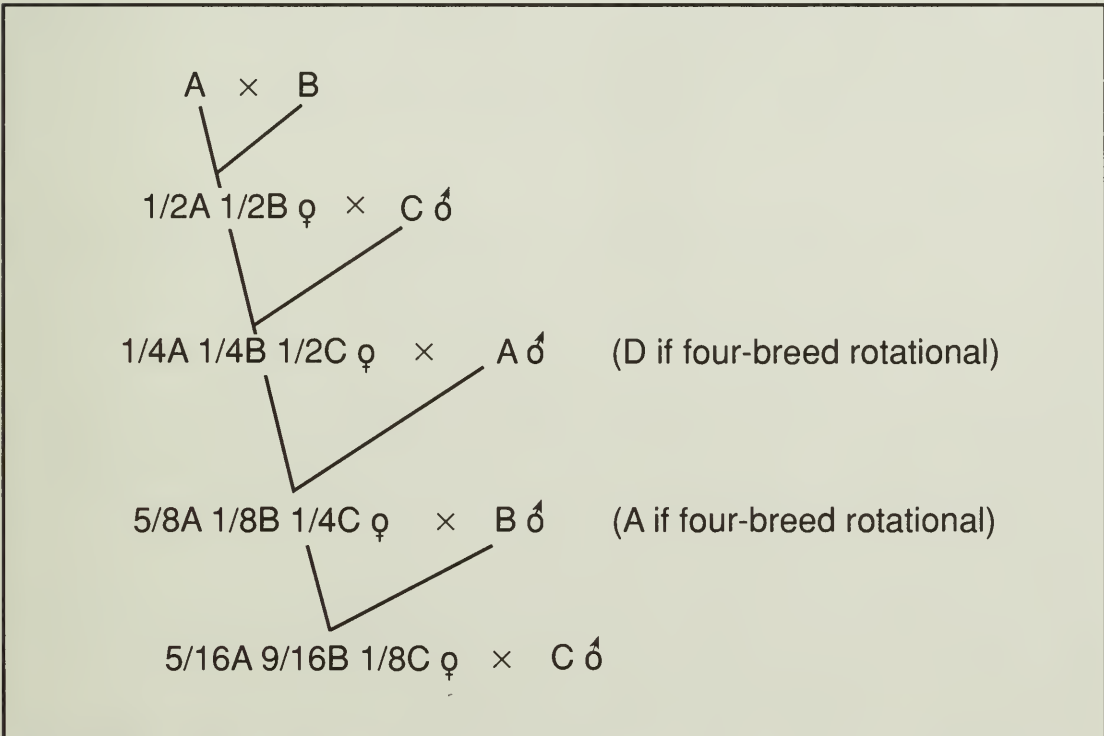


Fig. 9 Three- or four-breed rotational crossing.

Four-breed rotation Males from a fourth breed D are used on females of the combination $F_{(AB.C)}$. Thereafter males from breeds A, B, C, and D are used in succession for each new generation (Fig. 9).

After several generations of rotational crossing, the proportions of the different breeds in the genetic constitution of the crossbreds reach equilibrium. In two-way crosses, equilibrium means that 67% of the progeny's genes come from the breed to which backcrossing last took place, and 33% from the other breed. In three-way crosses, 57% of the genes come from the breed of the last-used male, 29% from the previous breed, and 14% from the third breed, which will be used for the next backcrossing. After equilibrium is reached, the highest proportion of genes in the genetic make-up of the progeny come from the males of the breed last used. The same rotation method can be used for crosses between inbred lines or strains within breeds.

The advantage of rotational crossing is that the females are always generated from within the flock, and the breeder exploits continuously the maternal heterosis of the crossbred females and the individual heterosis of the progeny. The disadvantage is the need to acquire the rams, or the cost of keeping small, purebred flocks to produce them.

Topcrossing

Topcrossing is a method in which inbred sires are mated to non-inbred dams. However, most breeders are less likely to use this method because inbred sires are not readily available in the market, and it takes a long time and costs much to produce these sires on the premises.

The advantage of using the inbred sires is their greater homozygosity (and subsequently ability to transmit favorable genes) in productive traits. The disadvantage is that inbred sires can also show the lower fertility and vigor associated with inbreeding.

Grading-up

Grading-up is to backcross to the same breed, generation after generation. The result is a gradual change, after which the population can be considered as a pure breed (Fig. 7). With each generation, the proportion of genes from the original population decreases to 50% of that present in the previous generation. For example, after four generations it decreases to 6.25% (1/16) and after five generations to 3.125% (1/32). Recently, American Finnsheep were developed using this method, and the breed was considered pure after four generations of grading-up.

The advantage of this system is that a breeder raising any breed, or even commercial ewes, can raise a flock of superior breed within a few generations by using only males from an improved or exotic breed. It is important to change the sires every generation to avoid inbreeding caused by using a sire on his daughters or granddaughters.

Combining crossing and selection

Crossing with recurrent reciprocal selection

The objective of this complicated system (Fig. 10) is to produce animals of two breeds or two strains within a breed, which give excellent performance when crossed. To use this system, first cross males from strain or breed A with females from strain or breed B, and vice versa. Then, evaluate the crossbred progeny for the important traits to be considered in the selection. Finally, use the selected parents whose crossbred progeny gave the highest performance to mate with animals of their own breed or strain. The outcome of such system is a gradual change in both populations to give better results in crosses with each other.

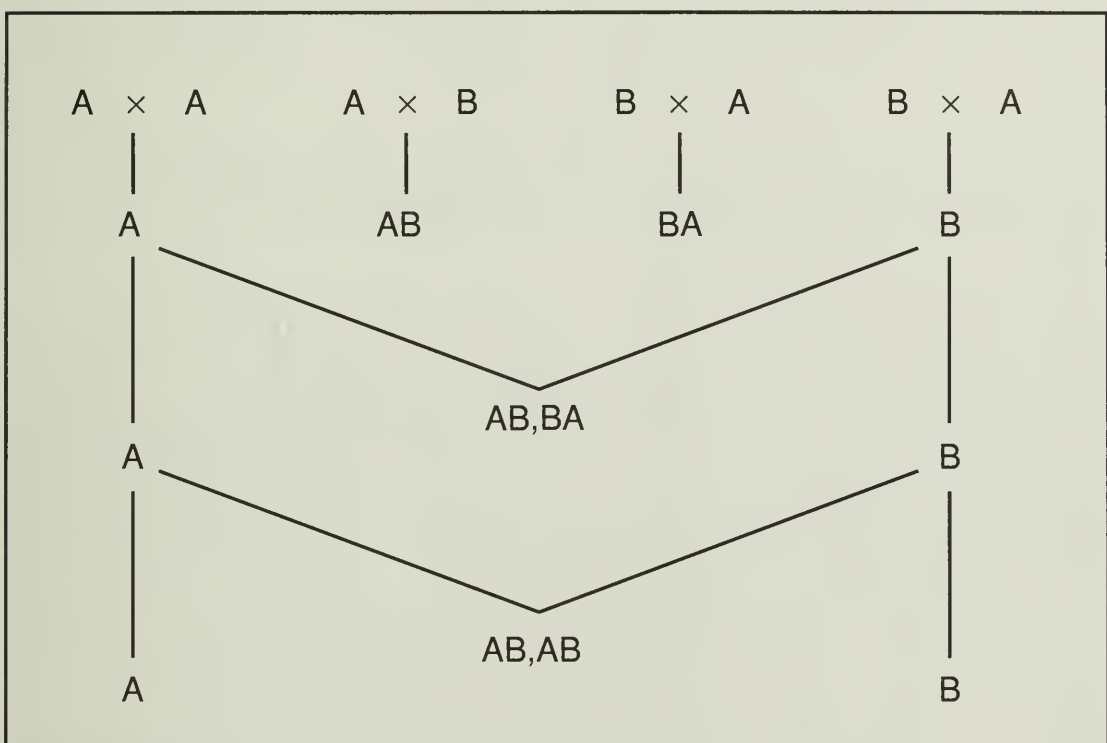


Fig. 10 Reciprocal recurrent selection scheme

Crossing to produce a new breed

Most present-day breeds of farm animals have been founded by crossing different breed types with each other in an attempt to combine their desirable traits in the new breed. A recent example of such a breed is the DLS breed developed by crossing Dorset, Leicester, and Suffolk breeds (Fig. 11). Each original breed contributed favorable characteristics to the cross. Also the three Arcott breeds were developed from crossing among numerous breeds. After the initial crossing, the populations are then closed and mated from within. Selection is often applied to maintain high level of the desirable traits.

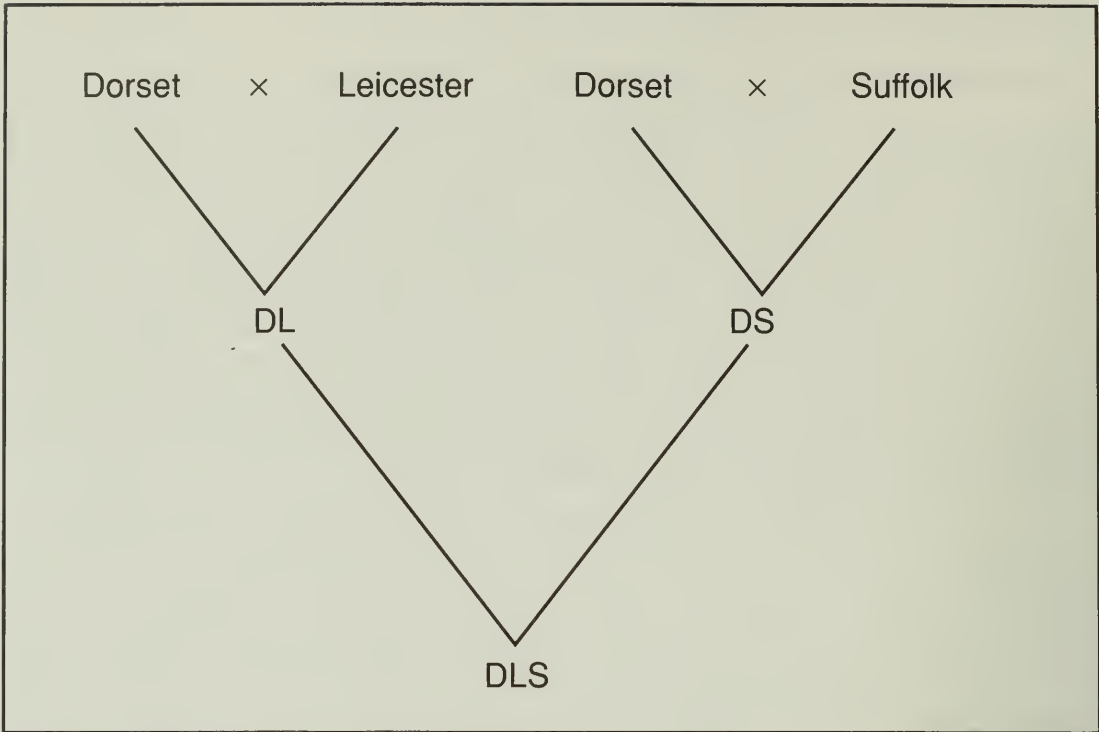


Fig. 11 Mating scheme of the DLS sheep.

General and specific combining abilities

When breeds are crossed, a certain breed may show superiority in crossing compared to other breeds. For example, if Suffolk, Hampshire, Oxford, and Dorset are crossed with various maternal breeds such as Leicester, Cheviot, and Romanov, and if most of the Suffolk crosses show superior productive traits, the Suffolk is referred to as having a superior *general combining ability*. In other words, Suffolk combine well with other breeds. If the cross Suffolk × Cheviot is superior in production, this combination can be identified of having a *specific combining ability*. Breeders are always advised to choose breeds that combine well with each other, a common term used for that is *nicking*.

Breeding plans using major genes

The discovery of major single genes responsible for economic traits, such as the Booroola gene for prolificacy in the Merino and double-muscling gene for meat production in the Texel, has provided new ways to improve sheep by incorporating these genes in popular breeds. Because the inheritance of these genes follows the simple rules of Mendel, breeders can see a remarkable improvement in a short time. To use the Booroola gene, for example, requires buying rams known to carry that gene and using them for crossing with

local sheep. If the rams are homozygous for that gene, i.e., carries two copies of the gene, all their progeny will carry one copy and will become prolific. If they are heterozygous for the gene, only half their progeny will be prolific.

To maintain prolificacy in the flock after introducing the gene, it is essential to close the flock and select replacements from within using only those carrying the gene and culling noncarriers. After a few generations, as the frequency of the Booroola gene increases, more and more animals become prolific, until such time when all the animals become homozygous for the Booroola gene. The secret of success for such a plan is the breeder's ability to properly identify the animals carrying the gene. The task is relatively easy in the case of females because they produce litters so their performance can be evaluated with a reasonable degree of accuracy. It is more difficult with males, and the breeder must depend on information about related animals and preferably progeny testing to identify carrier rams.

Record of Performance programs for maximizing genetic gain

The Federal-Provincial Record of Performance (ROP) programs, designed to help breeders identify and use superior animals for breeding, can have a profound long-term effect on genetic improvement of livestock. The ROP program for sheep was established in 1976. Participating breeders are required to record lambing dates and breed, number and sex of lambs, and body weights taken around 50 and 100 days of age. The information is submitted to regional offices and later fed to computers, which adjust these weights to a common basis and rank the animals according to their genetic merit for growth. Other useful statistics returned to the breeders include ewe productivity in terms of average number and weight of lambs born and weaned per ewe per year. Ram productivity expressed as average 50- and 100-day weights of all their progeny is also provided. Breeders are also provided with summary on the productivity of their flocks.

A new program called Expected Progeny Difference (EPD), begun in 1990, better assesses the breeding value of animals to assist breeders in making the right selection decisions. The EPD estimates the genetic value that an animal passes to its progeny; thus it measures the value of an animal as a parent. The advantage of EPD compared to the old ROP system is that it takes into account accumulated information of each flock since its inception. By using advanced statistical methods, all the information from relatives of each individual is considered in calculating the breeding value of that individual, even when these relatives are raised under different management within the flock (for example accelerated breeding, or intensive vs extensive feeding). One other advantage of this new

method is that information on the performance of an individual can be assessed even if its own records are missing. Because similar methods are used in dairy and swine production with noticeable genetic improvement in the Canadian herds, sheep breeders are advised to participate in these programs to make better choice of their breeding animals and maximize their genetic gain.

Conclusion

Knowledge of the principles of classical animal breeding and the use of its tools are definitely to the advantage of animal breeders. New technologies, such as the production of transgenic breeds in which genes with particular effects from other species are introduced to the genetic composition of other animals, can play a significant role in the future in speeding the progress or improvement of certain traits in certain animals. However, when such goals are achieved, the classical principles described in this booklet will still prevail if such improvement is to be maintained. Because the basis for genetic improvement (regardless of the method applied) is the proper identification and use of genetically superior animals, sheep breeders are encouraged to participate in national programs designed to identify such animals.

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