



**School of Agriculture food security
and Environmental Science**

**Department of Animal and Fisheries
Sciences**

AAN 308: ANIMAL BREEDING ¹

Lecture notes

Course Instructor:

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A course taught to third year students of Bachelor of Science in Animal Science and Bachelor of Science Agriculture Education and Extension (EGED)

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¹ Consultation: Tuesday 14.00- 16.00 hrs
Thursday 14.00- 16.00 hrs (with appointment)

COURSE OUTLINE

Course Description: Review of genetics; concepts of livestock improvement by manipulation of genetic makeup and environment of the animal; resemblance between relatives; genetic parameters and evaluation of genetic merit in animals using field data (prediction of breeding value); Selection; modes of selection, basis of selection, selection response, factors that influence genetic gain, multiple trait selection and correlated response to selection, mating systems, cross breeding; types of crossbreeding systems, heterosis and recombination loss, line breeding, inbreeding; calculating inbreeding; economic importance of inbreeding. Breeding strategies; nucleus breeding schemes, breeding biotechnologies; animal genetic resources, utilisation and conservation

Week	Topic	Subtopic
1	Introduction	Objectives of animal breeding Definition of terms
2	Genetic components of merit	Prediction of breeding values: The concept of heritability Usefulness of heritability estimates
3-4	Selection	What selection is all about? Basis for selection Selection response Factors that influence the rate of selection response Results from selection programmes
5	CONTINUOUS ASSESSMENT TEST 1	
5	Crossbreeding	The value of crossbreeding Genetic basis of heterosis Crossbreeding systems
6-7	Inbreeding	Calculation of inbreeding coefficients from pedigree Further Remarks about inbreeding coefficient Consequences of Inbreeding Prediction of Inbreeding from Population Size and Structure
8	Breeding systems	Open nucleus Closed nucleus
9	CONTINUOUS ASSESSMENT TEST 2	
9	Biotechnology in animal breeding	Molecular genetic biotechnologies
10	revision	

References

1. Douglas S. Falconer and Trudy F.C. Mackay, 1996. 4th Ed. *Introduction to Quantitative Genetics*. Benjamin Cummings. Pp 480
2. Michael Lynch and Bruce Walsh 1998. 1st Ed. *Genetics and Analysis of Quantitative Traits*. Sinauer Associates. Pp 980.
3. Richard M. Bourdon, 1999. 2nd Ed. *Understanding Animal Breeding*. Prentice Hall. Pp 538

INTRODUCTION

The livestock sector accounts for a substantial proportion of agricultural output in most countries of the world. As populations increase, and economic status of people improves, they tend to shift towards a diet based on more animal products. In response to expanding populations and the shift in consumption patterns, livestock output globally has been growing faster than other sectors of agriculture e.g.

- Faster growth rates of broiler chickens
- Improved egg quality in layers
- Good quality beef / meats from younger animals with improved carcass characteristics
- Increased milk production (better quality of milk etc)
- Great improvement in the pig industry

This pattern is expected to continue. Increases in output have been achieved partly by expanding numbers of animals, but more importantly by increases in efficiency of output. With finite resources and an increasingly vulnerable environment, it is critically important that growth in efficiency, rather than in numbers should be the dominant factor in the doubling of output of livestock products expected. Improvements in efficiency arise from **development, spread and adoption** of improved technologies for:

- Breeding
- Feeding
- Management
- Healthcare of animals

Additionally, improved technologies are required for

- Animal Welfare
- Conservation of genetic resources
- Management of livestock-environment interactions
- Efficiency of processing and marketing of livestock products

All these will enhance the nutritional and consumer safety aspects of livestock derived foods. Increasing efficiency of production is essential for:

- Economic and physical sustainability of different farming systems
- The long-term reduction in the cost of food

1.1 Objectives of Animal breeding

The objective of animal breeding is to **improve animal populations** (improve future generations of animals) --not to genetically improve individual animals. A population can be defined as a group of intermating individuals. The term can refer to a breed, an entire species, a single herd or flock, or even a small group of animals within a herd. To be able to improve a population, two basic tools are usually applied by animal breeders: **Selection and Mating**. Both involve decision making.

Selection can be defined as the process that determines which individuals become parents, how many offspring they may produce, and how long they remain in the breeding population. There are basically two types of selection:

Natural selection --selection that occurs in nature independent of deliberate human control

Artificial selection ---selection that is under human control

Through selection, animal breeders aim to *optimise the selection factors* in such a way as to maximise the genetic progress of breeding programmes.

In mating, one decides which of the selected males will be bred to which females that have been selected. The structure of a breeding industry and a breeder's place within that structure often influence that type of mating system that is adopted. For example in commercial poultry and pig production there is a clear division between seed stock and commercial sectors, hence it is common to find breeders of pure-bred seed stock. The whole aim in these systems is to take advantage of all breeding methods that will increase the efficiency with which animal products are produced.

Selection and mating are interdependent--animals are selected first, then mated to produce offspring that comprise the next generation. Used together, genetic gain in traits of economic importance is achievable in livestock populations.

1.2 Some basic concepts/definition in animal breeding and genetics

Simply inherited and polygenic traits

A **simply inherited trait** is a trait that is affected by only a few genes e.g. Coat colour and presence of horn. Such traits have two common characteristics: **First**, phenotypes for these traits tend to be "either/ or" in nature (categorical/ qualitative). **Second**, the traits are affected very little by the environment. [a cow either has horns or is polled, a Labrador is either black, chocolate or yellow].

A **polygenic trait** is a trait affected by many genes, no single gene having an overriding influence. Phenotypes for polygenic traits are typically quantitative in their expression (show continuous expression). Such traits are generally numerically measured-eg. 250 kg weaning weights, 7500kg lactation yield etc.

Note:

The distinction between genes concerned with *Simply inherited* traits and *metric traits* lies in the magnitude of their effects relative to other sources of variation.

A gene with an effect large enough to cause a *recognisable discontinuity* even in the presence of segregation at other loci and of non-genetic variation can be studied by "Mendelian" methods. A gene whose effect is not large enough to cause discontinuity cannot be studied individually. The terms *Major gene and Minor gene* are used for convenience to distinguish between genes. There are however no fundamental differences between genes.

The basic tools of animal breeding (selection and mating) are the same for all types of traits. *However, very different breeding approaches are taken to improve simply inherited and polygenic traits.* The difference in approach is a function of the **number of genes involved**. The more the genes affecting a trait, the more difficult it is to observe the effects of individual genes, and thus the less specific information we have about those genes. The amount of available information affects the way we **characterise genotypes** and thus determine the animal breeding technology to use.

1. GENETIC COMPONENTS OF MERIT

Animal breeding in a nutshell

WHERE TO GO?	OBJECTIVES -What types of animals to breed for -Economic value of commercial traits
HOW TO GET THERE?	QUANTITATIVE GENETICS SELECTION THEORY CROSSING THEORY -Which animals to breed from -Mate allocation
GETTING THERE	IMPLEMENTATION -Education -Industry structures -Business structures

Whereas *Population Genetics* is concerned with the *fitness* of different genes (i.e. their likelihood of surviving and increasing in frequency over generations), *quantitative genetics* is concerned with the *merit* of different genotypes (i.e. their value to as in agricultural terms). The merit of different genotypes is addressed by considering a single locus (Falconer Ch.7):

Single Locus Model of Genotypic Merit

The object of this section is to illustrate:

- The concept of *Genetic value* - the value of an animal's genes to itself. This will also help show the effects of gene frequency (p and q) on the population mean merit.
- The concept of *Breeding value* - the value of an animal's genes to its progeny. This is of greater interest to us, as it encompasses the basis of ongoing genetic improvement

Genetic Value And Breeding Value - The Difference.

Consider genotype A_1A_2 :

Its heterozygosity means its carrier enjoys the effect of dominance in its **GENETIC VALUE**
-The value of its genes to itself

Its heterozygosity cannot be transmitted to its progeny - because it cannot give both alleles to any one progeny. Thus the value of its progeny is different from the value of its genes to itself

Its **BREEDING VALUE** - the value of its genes to its progeny, depends on the single genes it can transmit, A_1 and A_2 . Each of these has an average effect on progeny.

Its **BREEDING VALUE** - is thus the sum of average effects of the genes it carries.

2. SELECTION

Selection is a method used by breeders to confer long term genetic changes in an animal population. It is the process that determines which individual become parents, how many offsprings they produce and how long they remain in the breeding population. Selection is considered as either natural; one that occurs in nature independent of deliberate human control or artificial; one that is under human control. Another terminology that is closely associated with selection is culling. Culling is the process that determines which parents will no longer remain parents.

The objective of selection is to change the average performance of a population by increasing the frequency of the plus alleles at loci that influence the trait. However, selection must be based on phenotypic so our ability to identify genetically superior individuals will be less than perfect.

Artificial Selection - Truncation Method

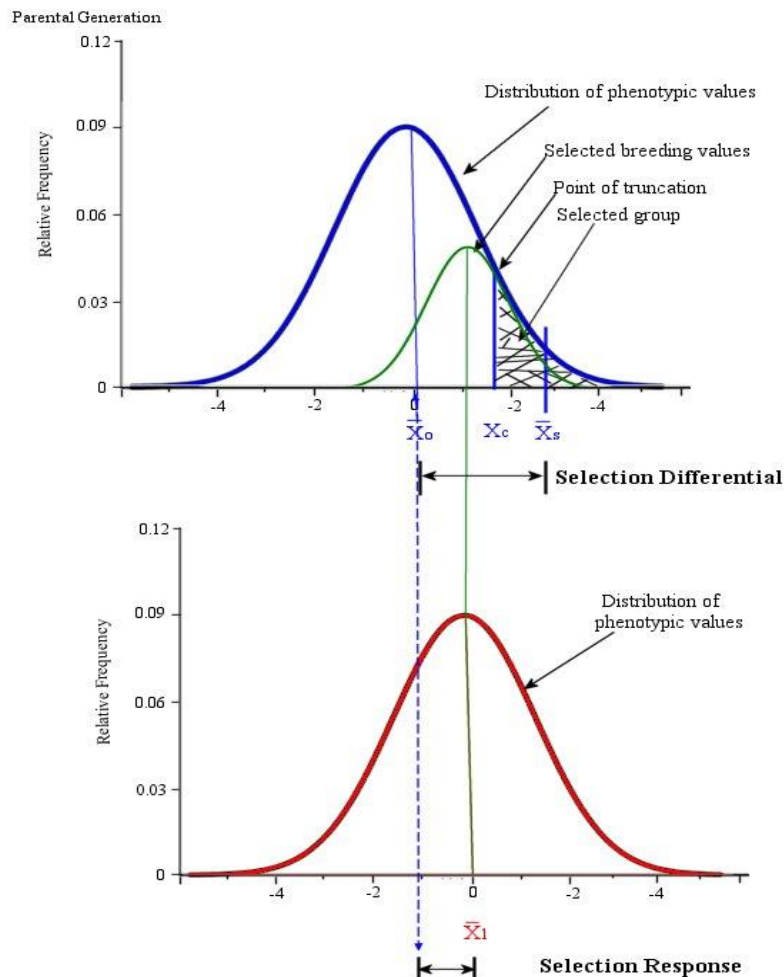


Figure 4.1: normal distributions showing specific characteristics as they relate to truncation selection; upper distribution is for the parental (selected) generation, the lower distribution is for the progeny of selected parents

Generally the individuals to be selected are identified as those with performance above some minimum level set by the breeder. This minimum level of performance, referred to as the *point of truncation*, and labeled X_c in the figure below, defines a point on the distribution of phenotypic values that partitions the population into two groups; those to be selected as breeding individuals (selected group) and those to be discarded (unselected group). The average performance of the selected group is labeled X_s , the mean of selected group.

Selection Pressure

Selection response is dependent on identifying superior individuals as parents for the next generation. There are two methods used to measure the phenotypic superiority of selected individual: selection differential and selection intensity. The two measures are closely related for traits with values distributed as expected for the normal distribution; the relationship will be discussed under the description of selection intensity

Table 4.1: Definition of symbols and values for a numerical example, using hypothetical values for body weight of trout

Symbol	Definition	Example
M_0	parental population mean	12.00
σ	standard deviation	1.60
X_c	point of truncation	14.00
X_s	mean of selected parents	14.50
M_p	mean of offspring of selected parents	12.25
SD	selection differential	$14.50 - 12.00 = 2.50$
i	selection intensity	$2.50 \div 1.60 = 1.56$
SR	selection response	$12.25 - 12.00 = 0.25$
h_R^2	realized heritability	$0.25 \div 2.50 = 0.10$

Selection Differential (SD): The phenotypic superiority of the selected group is calculated as the difference between the mean of the selected group and the mean of the parental population to which the selected individuals belong. For the example, as outlined in Table 4.1, the selection differential is

$$SD = 14.50 - 12.00 = 2.50 \text{ kg}$$

The sign of the selection differential indicates the direction of selection. A positive value indicates selection for larger phenotypic values while a negative selection differential would indicate selection for smaller phenotypic values.

Selection Intensity: Notice from examination of Figure 4.1, on the previous page, that the selected group constitutes a fixed proportion of the total population. Also, it should be clear that the size of the selection differential (the distance from M_0 to X_s), depends on the phenotypic variance of the trait. The assumption is made that the proportion of the population selected will provide the number of breeding individuals needed to maintain population size.

Given these facts about the selection differential and the normal distribution, it is possible to evaluate selection pressure in terms of σ_P , phenotypic standard deviation units. The selection pressure stated in standard deviation units is called selection intensity, and is defined as i . It represents the phenotypic superiority of the selected group measured as number of standard deviations between the mean of the population and the mean of the selected group. Thus, it follows that $SD = i\sigma_P$, or stated in words, the selection differential is equal to the product of the selection intensity and the phenotypic

standard deviation. For the example in Table 4.1, the selection differential is 2.50 and the standard deviation is 1.60 giving a selection intensity of $i = 2.50 \div 1.60 = 1.56$ standard deviations.

The practical significance of selection intensity is two-fold. First, selection intensity is in standard deviation units so it is possible to compare selection pressures for different traits regardless of the type of units used to measure performance. For example, consider selection for two traits in dairy cattle; milk production (lb) and percent fat (%) with selection differentials of +500 lb and +0.05 %, respectively. Since the units of measurement are very different it is difficult to appreciate the relative selection pressure applied for each trait. However, if the standard deviations are 3142 lb for milk production and 0.389 % for fat percent, the selection intensities for the two traits are

Milk: $i = 500 \div 3142 = 0.16$ standard deviations

Fat: $i = 0.05 \div 0.389 = 0.13$ standard deviations

Clearly, comparing the selection differentials standardized to standard deviation units shows the selection pressures applied for these two traits are very similar.

Predicting Selection Differential: The second significant aspect of selection intensity is that it can be used to predict the selection differential from knowledge of the replacement rate desired for the population and the reproductive rate of the species. For example, if the goal is to replace 100% of 200 breeders (males + females) each generation, and 100 matings (one male + one female) will produce 1000 adult progeny, it would be necessary to select 20% of progeny as replacement breeders. It is possible to convert this proportion selected into selection intensity, i , because there is a direct relationship between proportion of a population and number of standard deviations between means, given the characteristics of the normal distribution.

The table given in Table 4.2 gives examples, taken from a table of the normal curve, of the relationship between percent of a population selected and number of standard deviations the mean of the selected group will differ from the mean of the population (i). Using the equation for SD and the values in the table, it is possible to project the size of a selection differential from a knowledge of the phenotypic standard deviation and the proportion of the population that must be selected to maintain the population size. We will use this knowledge in the next section discussing ideas of selection pressure differing between sexes.

Different Selection Intensities in Two Sexes: For most animal species, it is possible to select males more intensively than females because fewer males than females are needed for reproduction. For example, in range beef production it is likely that only 10% of the male progeny will be needed as replacement bulls, while it is likely about 50% of the female progeny will be retained as replacements.

Table 4.2. Selection intensity (I) and its relationship to proportion of a population selected. The values given assume selection in a very large population.

Percent Selected	Selection Intensity (i)
1	2.67
5	2.06
10	1.75
20	1.40
50	0.80
80	0.35

Consider selection for beef cattle weaning weight of individual calves as the selection criterion. If the phenotypic standard deviation of 40 kg, the expected selection differential, using values listed in Table 4.2, are:

Males:

10% selected corresponds to $i = 1.75$, and
 $SD_m = (1.75)(40) = 70$ kg

Females:

50% selected corresponds to $i = 0.80$, and
 $SD_f = (0.80)(40) = 32$ kg

Population:

Then the selection differential for the population is the average of the values for males and females because their genetic contribution is equal for each offspring.

$$SD_p = (SD_m + SD_f) / 2$$

$$SD_p = (70 + 32) / 2 = 51 \text{ kg}$$

Although selection differentials are known during an actual selection program, it often is of interest to predict selection differentials during the planning stage of a selection program so population size and replacement rates can be established to ensure an effective selection program.

Selection Response and Realized Heritability

Selection Response

The effectiveness of a selection program can be evaluated by comparing average performance in the parental and progeny generations. Remember the mean performance of a population is the best estimate of the average genetic value of the population. The change in average performance between consecutive generations is referred to as either *genetic gain* (ΔG) or *selection response* (SR) achieved in one generation. The selection response, shown for the example in Figure 1 on a

previous page, is the difference between the mean of offspring population, X_o , and the mean of parental population, X_p , or,

$$SR = (X_o - X_p) = 12.25 - 12.00 = 0.25 \text{ oz}$$

As pointed out earlier, the mean performance of a population also represents the mean genetic value of the population. Therefore in a selection program, since progeny represent random sampling of parental genes, the mean of the offspring generation represents the mean breeding value of the selected parents. We can assume also that the breeding values of selected parents will be distributed around their mean breeding value. This notion is shown in Figure 4.1 as the arbitrary distribution given as an inset to the distribution of the parent population and labeled "Selected Breeding Values."

Note that the response to selection (0.25 oz) in our example (Table 4.1) is considerably less than the selection differential (2.50 oz). Clearly, the superiority of the selected group over the mean of the parental population was not entirely due to additive genetic superiority. In addition to a bias imposed by environmental effects, the superiority could result from non-additive genetic effects. On average, we would expect non-additive genetic and environmental deviations for the selected individuals to be biased in the direction of selection; positive for selection to increase phenotypic values and negative for selection to decrease phenotypic value. This bias is expected for environmental effects even though overall environmental effects are random; selected superior phenotypes do not a random sample of genotypes. Consequently, the performance of progeny is never as great as one would predict from the performance of their parents. This observation is often referred to as a "regression toward the mean" since the offspring mean always "tends toward" the mean of the parental population.

Realized Heritability

In an earlier discussion, it was shown that heritability is a measure of the level of performance expected for progeny based on the performance of their parents since it represents the regression of phenotypic value on breeding value. Therefore, it seems reasonable to think of the difference between the performance of parents and progeny as a reflection of the heritability of the trait. In fact, it is possible to estimate the heritability of the trait under selection as the ratio of the selection response to the selection differential. This parameter is called the *realized heritability*. For the example in Table 4.1, the realized heritability for the single generation of selection is,

$$h_R^2 = \frac{SR}{SD} = \frac{0.25}{2.50} = 0.10$$

Thus, for our hypothetical example, the genetic change achieved was only 10% of the superiority of the parents. Often, heritabilities estimated from selection experiments are the most reliable estimates available in the scientific literature.

Factors Determining rate of Change from Selection

There are four basic elements that determine rate of response to selection; the key equations tie the four together into a simple paradigm. First let's describe the four elements before developing the equations: (1) accuracy of selection, (2) intensity of selection, (3) genetic variation, and (4) generation interval.

1. Accuracy of Selection

Accuracy of selection refers to the reliability of estimates of true breeding value. We have learned from an analysis of heritability that the strength of the relationship between true breeding value and predicted breeding value is the correlation between the two values. Clearly, since selection depends on identifying superior individuals as future parents, the accuracy of selection will be determined by reliability of the estimation procedure used to rank individuals. The simplest procedure is to rank on the basis of phenotypic value, in which case, the accuracy of selection would be the heritability of the trait used for ranking. However, this approach may not be effective for traits with low heritability or for sex limited traits; other methods of defining a more appropriate phenotype can be used to improve accuracy of prediction.

The breeder can influence the accuracy of selection indirectly through maintaining good management conditions to minimize environmental variation that cannot be categorized. In addition, care in measuring performance with minimal error reduces non-genetic variation, and maintaining accurate pedigree information and performance records eliminates error of identification. Minimizing non-genetic variation has the effect of improving the heritability of the phenotypic values by maximizing the ratio of additive genetic variance to phenotypic variance.

2. Selection Intensity

Rate of genetic change will be affected by the amount of effort placed on “keeping” only the very best individuals as future breeders. Selection intensity is best defined as the proportion of individuals available as future breeders that is kept to produce the next generation. For example, if as sheep breeder was able to keep only the “top” 10% of individuals in the flock as future parents, the effort to keep only the best would be far greater than if 70% of potential breeders were used to produce the next group of lambs. Selection intensity is related to the performance difference between those selected as breeders and the pool of potential breeders; we will address this relationship after we develop the key equations.

Two factors tend to control selection intensity; the reproductive rate of the species, and the number of animal with performance records. Reproductive rate determines the proportion of progeny that must be used as replacement breeders to maintain a constant population size. For example, the proportion of female progeny needed as replacements is higher for cattle than for pigs, which is higher than that of chickens, simply because as a rule cattle produce only one offspring per mating, pigs may produce 10 or 12 offspring per mating and chickens can produce as many as 25 or 30 offspring per mating.

Number of animals with performance records can be limited by reproductive rate, but more often it is determined by economics, the cost of obtaining the performance records. As an example, compare the effort required to obtain information on growth rate and feed conversion ratios for pigs. The growth rate phenotypic value can be obtained by simply weighing each pig at the beginning and at the end of the growth period, maybe from weaning to market age. Feed conversion ratios, on the other hand, require that feed intake be measure for each pig, as well as growth over the test period; it seems reasonable to assume that it would take a great deal of effort to obtain feed intake values for even a few tens of pigs. To see the effect on selection intensity, assume a swine breeder typically needs 200 replacement females each year, that 2000 pigs are test for growth performance, but phenotypic values for feed conversion would be available on only 500 pigs. The selection intensity for growth would be 200/2000 or about 10% selected (90% culled), while 200 out of 500 or about 40% would be selected based on feed conversion ratios (only 60% culled).

3. Genetic Variation

There must be genetic differences among individuals for selection to be effective. Thus, it follows that the opportunity to achieve genetic change will be enhanced by high levels of additive genetic variation. However, there is little the breeder can do about the level of genetic variation within the population after selective improvement has been initiated. It is advisable to begin a new breed improvement program with as high a level of genetic variation as possible; sometimes this can be achieved by out-crossing to unrelated groups to bring additional genetic material into the population. If the out-crossing is not done until after some generations of selection, it becomes difficult to identify individuals from other populations that are genetically superior to the average breeding value of the indigenous population.

4. Generation Interval

Breeders in a population must be replaced by their offspring if genetic change is going to occur over the long-term. Generation interval refers to the length of time it takes to replace, or turn-over, the breeding population. Stated another way, generation interval is the time taken to replace one generation with a new generation. This factor is associated directly to reproductive rate, age at maturity and age at culling old breeders. A chicken breeder can replace all individuals every calendar year while a mouse breeder can achieve between two or more generations on one year. Mice are sexually mature in a few months after birth and is one of the main reasons mice have been a popular laboratory species for research on quantitative genetics. However, replacing a generation of beef or dairy cattle can take six to eight years and the time is longer for horses.

The Key Selection Equations

1. Genetic Change per Generation

Equation #1 defines prediction of genetic change per generation. We will discuss each term in the Key Equation

$$\Delta G = r_{AA'} i \sigma_A$$

1. ΔG : the symbols delta and G will be used consistently to represent genetic change per generation
2. $r_{AA'}$: the accuracy selection; refers to correlation between true breeding values (A) and estimated breeding values (A'). This parameter can take on many forms depending on the type of phenotype used as the selection criterion, such as individual phenotypes, averages of repeat records, average performance of progeny.
3. i : the selection intensity. The “amount of selection” is most often measured as the difference between the mean of the population (μ_0) and the mean of the selected parents (X_s) and is known as the selection differential (SD), where

$$SD = (X_s - \mu_0)$$

Selection differential can be converted to a standardized variable, known as *selection intensity*, by dividing the selection differential by the phenotypic standard deviation of the trait. Thus, expressed in standard deviation units, we have that selection intensity,

$$i = \frac{SD}{\sigma_P}$$

4. σ_A : the additive genetic standard deviation, a measure of level of differences among breeding values of the animals in the population. With regard to selection, the important differences are variation among breeding values of the animals. As σ_A increases, the superiority of the best animals increases relative to the mean of the population; with little variation the superior animals are only slightly above the mean.

2. Annual Genetic Change

Equation #1 describes genetic change in per generation. An animal breeder is more interested in the change per year. The time to turn over a generation is defined as the average age of the parents when the offspring are born and is referred to as *generation interval* (L). For cattle and horses this can range from 5 to 8 years while in chickens from 1 to 1.5 years.

To develop *Equation #2*, genetic change per year, we need simply divide the right hand-side of Key Equation #1 by the generation interval (L), to obtain the estimated genetic change per year (t), as

$$\Delta G_t = \frac{r_{AA'} i \sigma_A}{L}$$

When selection is solely on a single measurement of each individual's phenotype, the key equations can be modified to describe genetic change in terms of heritability and phenotypic variation. Through algebraic manipulation Equation #1 is modified to give rise to Key Equation #3 describing expected response to *phenotypic selection*. Genetic change per generation can be predicted by dividing Equation #3 by generation interval

Equation #3 for phenotypic selection is

$$\Delta G = h^2 i \sigma_p$$

Adjusting of Different Selection Intensities in Sexes

What if the selection intensity differs between the sexes? This is quite reasonable when you consider that most animal populations are polygamous resulting in the need for fewer males than females to reproduce the population. If fewer males than females are selected as future parents, the selection intensity for the males will be greater than the females. Because male and female parents make equal genetic contributions to each progeny, the actual selection pressure, corrected for differences between the sexes, can be calculated as the simple average of selection pressure applied to each sex.

Thus, in terms of selection differential, the corrected value *Equation #4* is,

$$SD_c = \frac{SD_m + SD_f}{2}$$

whereas the corrected value in terms of selection intensity, *Equation #5* is,

$$i_c = \frac{i_m + i_f}{2}$$

Where: SD_m = selection differential for males; SD_f = selection differential for females; i_m = selection intensity for the males; and i_f = selection intensity for the females.

$$\Delta G_{gen} = \frac{i_m + i_f}{2} h^2 \sigma_p$$

The corrected selection pressure can then be applied in the equations for genetic change (Equation #1, #2 or #3); these equations also may need to be adjusted for generation interval differences between sexes to obtain estimates of annual genetic change.

EXAMPLE- yearling weight in beef cattle

Average yearling weight of 100 bulls : $\bar{X}_m = 300\text{kg}$ $\bar{X}_f = 275\text{Kg}$

$h^2 = 0.25$ $\sigma_p = 30\text{kg}$

What is expected average weight of the top 10 bulls?

$S_m = i \sigma_p$ $p_m = 10/100$ giving $i_m = 1.755$, $\sigma_p = 30\text{kg}$

$S_m = 1.755 \times 30 = +52.65\text{kg}$ superior, over 300. Answer = 352.65Kg

What is response to selecting these bulls over random cows?

$R = \frac{1}{2}(i_m + i_f)h^2\sigma_p$ -where i_f is expected to be zero

$R = \frac{1}{2} (1.755 + 0) \times 0.25 \times 30 = 6.58\text{kg response.}$

Note: This gives an expectation of 300 +6.58kg for male progeny and 275 + 6.58kg for female progeny.

What is response to selecting these bulls over the best half of the heifers?

$p_f = 0.5$ giving $i_f = 0.798$

$R = ih^2\sigma_p = \frac{1}{2} (1.755 + 0.798) \times 0.25 \times 30 = 9.57\text{kg response.}$

Note: This give an expectation of 300 +9.57kg for male progeny and 275 +9.57kg female progeny.

Sex Differences in Generation Interval

Differences can exist in the generation interval for the two sexes. For example, with species with low reproductive rates, males are often younger than females since the replacement rate for males can be more rapid than for females. This difference is handled in the same manner as differences in selection intensity, by calculating the average for the two sexes.

The adjustments for differences between males and females in selection pressure and generation interval can be applied simultaneously to a create new equation. Below is a form of Equation #3 adjusted for the combined effects of differences in selection intensity and generation interval *Equation #6*.

$$\text{Response per year} = \frac{i_m + i_f}{L_m + L_f} h^2 \sigma_p$$

A similar equation can be derived for selection differential. The reader is reminded that the value "2" appears in the numerator and denominator of the adjusted equations so can be dropped from the final equation.

EXAMPLE: Fleece weight in sheep.

Consider a 1000 ewe flock with an age structure typified by the numbers in the table below. Notice that, fairly typically, we keep rams 2 years, keep ewes 6 years, and drop first progeny at 2 years. Mating ratio is 1 ram to 50 ewes, and there is some mortality.

The question is, what is the predicted response to selection per year

Assume.

Heritability 0.3

Standard Deviation 0.4kg
Weaning rate 0.8

Age at drop of progeny	2	3	4	5	6	7	TOTAL
No. of rams:	12	8					20
No. of ewes:	250	200	180	150	120	100	1000

Calculation of predicted response per year to selection

$$L_m = \frac{12 \times 2 + 8 \times 3}{12 + 8} = 2.4 \text{ years} = \text{average age of rams 'dropping' progeny}$$

$$L_f = \frac{250 \times 2 + 200 \times 3 + 180 \times 4 + 150 \times 5 + 120 \times 6 + 100 \times 7}{250 + 200 + 180 + 150 + 120 + 100} = 3.99 \text{ years}$$

1000 ewes give $0.8 \times 1000 =$ progeny, 400 male and 400 female

$p_m = 12$ young rams selected out of 400 available $= 12/400 = 0.03$

From tables, $p_m = 0.03$ gives $i_m = 2.268$

$p_f = 120/400 = 0.3$ giving $i_f = 1.159$

$$\frac{i_m + i_f}{L_m + L_f} \times h^2 \times \delta_p = \frac{2.268 + 1.159}{2.4 + 3.99} \times 0.3 \times 0.4 = 0.0643$$

$R_{\text{year}} = 0.0643$ kg increase in fleece weight predicted per year

We have now tools to compare alternative selection programs!

An alternative to the previous program is to cull older ewes and retain more young ones

Lower female selection intensity decreases R_{year}
Shorter generation interval increases R_{year}

It turns out that if we cull ewes after 6 years, and retain some more 2 year old ewes, the generation interval decrease offsets the loss in selection intensity, and the annual genetic gain would increase.

However, if we would cull ewes older than 4 years of age, we would need to keep nearly all newly born female lambs as breeding females (no selection intensity left) and this breeding program would be less optimal.

Notice that the optimal strategy depends on survival rates, and female fecundity,. For example, if females would leave more lambs each, we need to keep less breeding females, resulting in higher

female selection intensities. The resulting strategy would have lower generation intervals when breeding ewes leave more progeny.

Selection intensity table

Table 1. Truncation point (x_0) and selection intensity (i) for different proportions selected (p in %) in large samples. Based on Falconer and Mackay (1996)

p (%)	x_0	i	p (%)	x_0	i	p (%)	x_0	i
0.01	3.719	3.960	1.0	2.326	2.665	16	0.995	1.521
0.02	3.540	3.790	1.2	2.257	2.603	17	0.954	1.489
0.03	3.432	3.687	1.4	2.197	2.549	18	0.915	1.458
0.04	3.353	3.613	1.6	2.144	2.503	19	0.878	1.428
0.05	3.291	3.554	1.8	2.097	2.459	20	0.842	1.400
0.06	3.239	3.507	2.0	2.054	2.421	21	0.806	1.372
0.07	3.195	3.464	2.2	2.014	2.386	22	0.772	1.346
0.08	3.156	3.429	2.4	1.977	2.353	23	0.739	1.320
0.09	3.121	3.397	2.6	1.943	2.323	24	0.706	1.295
0.1	3.090	3.367	2.8	1.911	2.295	25	0.674	1.271
0.12	3.036	3.313	3.0	1.881	2.268	26	0.643	1.248
0.14	2.989	3.273	3.2	1.852	2.243	27	0.613	1.225
0.16	2.948	3.234	3.4	1.825	2.219	28	0.583	1.202
0.18	2.911	3.201	3.6	1.799	2.197	29	0.553	1.180
0.20	2.878	3.170	3.8	1.774	2.175	30	0.524	1.159
0.22	2.848	3.142	4.0	1.751	2.154	31	0.496	1.138
0.24	2.820	3.117	4.2	1.728	2.135	32	0.468	1.118
0.26	2.794	3.093	4.4	1.706	2.116	33	0.440	1.097
0.28	2.770	3.070	4.6	1.685	2.097	34	0.413	1.078
0.30	2.748	3.050	4.8	1.665	2.080	35	0.385	1.058
0.32	2.727	3.030	5.0	1.645	2.063	36	0.359	1.039
0.34	2.706	3.012	5.5	1.598	2.023	37	0.332	1.020
0.36	2.687	2.994	6.0	1.555	1.985	38	0.306	1.002
0.38	2.669	2.978	6.5	1.514	1.951	39	0.279	0.984
0.40	2.652	2.962	7.0	1.476	1.918	40	0.253	0.966
0.42	2.636	2.947	7.5	1.440	1.887	41	0.228	0.948
0.44	2.620	2.932	8.0	1.405	1.858	42	0.202	0.931
0.46	2.605	2.918	8.5	1.372	1.831	43	0.176	0.913
0.48	2.590	2.905	9.0	1.341	1.804	44	0.151	0.896
0.50	2.576	2.892	9.5	1.311	1.779	45	0.126	0.880
0.55	2.543	2.862	10	1.282	1.755	46	0.100	0.863
0.6	2.512	2.834	11	1.227	1.709	47	0.075	0.846
0.65	2.484	2.808	12	1.175	1.667	48	0.050	0.830
0.70	2.457	2.784	13	1.126	1.627	49	0.025	0.814
0.75	2.432	2.761	14	1.080	1.590	50	0.000	0.798
0.8	2.409	2.740	15	1.036	1.554	60	-0.253	0.644
0.85	2.387	2.720				70	-0.524	0.497
0.90	2.366	2.701				80	-0.842	0.350
0.95	2.346	2.683				90	-1.282	0.195
1.0	2.326	2.665				95	-1.645	0.109

Basis of selection decisions

Selection of animals on the farm could be made on the basis of various information sources (selection criteria). These include:

1. Own information: information on the bull's own performance could be used to evaluating it. However this information given is less accurate in traits the low heritability e.g. fertility traits. In addition, the criterion is sex limited for instance the bull has no information on milk yield since this trait is only exhibited in female.
2. Progeny information: this involves selection on the basis of performance information from the offsprings of the candidate animal. In this case animals with better performing offsprings are chosen. Since the method involves taking records of offsprings, the animals must have offsprings in performance to be considered. It therefore takes a lot of time (long generation interval). However this is the most accurate way of getting the best animal.
3. Sib information: information from the either full or half sib females could be used. Given the low proportions in the relationship, the level of accuracy towards getting the right animal is reduced
4. Pedigree information: this involves use of the animals' parents and grandparents information to select the best performing candidate. Since the records of dams' performance are available by the time the bulls are born, it saves on time.
5. Molecular information: this involves identifying the genes that influence the traits in question and selecting only those animals that have the genes. The method is very accurate although it is expensive

3. MATING SYSTEMS

After selection, the selected animals can only become parents by being joined to produce offspring. In this case, pure breeding or crossbreeding mating systems may be used. Pure breeding systems are important if additive genetic potential of the animal is of paramount importance to be exploited. However, situation may arise where the additive genetic potential of the animal is less important and instead other within and between loci interaction of genes are prominent. In this case, other mating strategies are utilised such as crossbreeding to exploit heterosis.

Crossbreeding

The value of crossbreeding

1. The averaging of breed effects- e.g. to get an animal of an intermediate size to fit a particular pasture cycle or market demand.
2. Direct heterosis. Crossbred individual often exhibit heterosis. Heterosis is measured as the extra performance of the crossbreds over the weighted average of their parent breeds. The percentage increase in performance ranges about 0- 10% for growth traits and 5- 25% for fertility traits. The effect of heterosis on the total production system can be even more than this, as effects accumulate over traits.
3. Maternal heterosis. Crossbred dams can exhibit considerable heterosis in their ability to raise many, fast growing, and viable offspring.
4. Sire-Dam complementation. A good crossbreeding system aims to use breeding females which are small (but not so small for dystocia to be a problem) as well as prolific. When a large breed of sire is used the proportion of feed directed to growing animals is increase and the production system benefits accordingly.
5. Possibly cheap source of breeding animals. This is evident in the Australian prime lamb industry, where surplus Merino ewes are bought cheaply and crossed with Border Leicester rams to produce prime lamb dams. In Kenya, cast/cull for age Red Maasai ewes are still good for crossing to Dorper rams to give first cross ewes which can act as prime lamb dams. They are cheap to buy in and this might help drive Kenya's meat sheep crossing structure.
6. Potentially widest use of genetic resources- including increased selection intensity and reduced inbreeding.

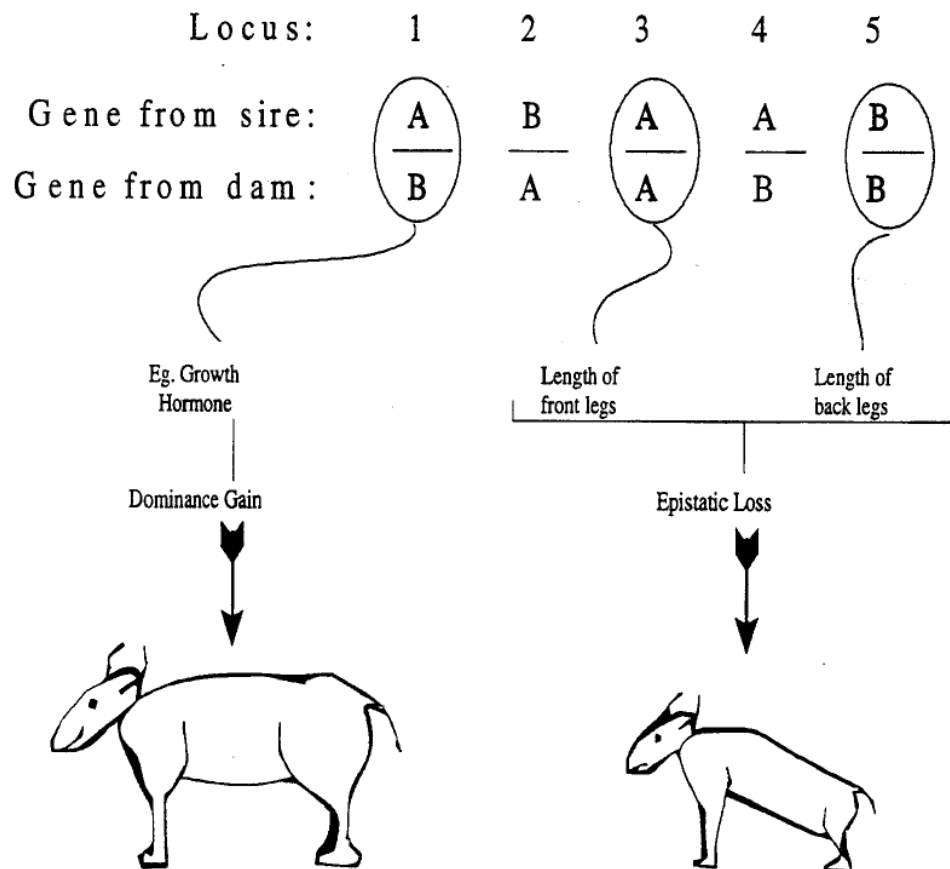
The genetic basis of heterosis

We need to know this to predict the value of untested genotypes. For example, for a trait with no maternal effects we may have measures of the performance (MERIT) of a number of crossbred genotypes.

Genotype	Merit	=	Average of parental breeds	+	heterosis
Breed A	10	=	10	+	0
Breed B	12	=	12	+	0
Breed C	16	=	16	+	0
AxB	16	=	11	+	5
Ax (BxC)	17	=	12	+	5
Ax (AxB)	?				?

There is no direct measure of the backcross A x (AxB), so we need to be able to predict how much heterosis it will express to predict its value. For this we need to know the genetic basis of heterosis.

Mix genes from different breeds (A and B) in one individual



Dominance. Where the individual's parents come from two different breeds, the individual will carry a wider range of genes sampled from two breeds rather than just one. It is thought that this better equips the individual to perform well, especially under a varying or stressful environment. We would thus expect dominance to be a positive effect and there is much evidence to support this.

Epistasis. When we cross breeds, genes find themselves having to interact or ‘cooperate’ with other genes which they are not used to. The crossbred animal may therefore be out of harmony with itself and we predict that epistasis, if important, is a negative effect.

The dominance model of heterosis

If heterosis were due to ‘breed dominance’ alone:

Breed dominance is greatest when all loci consist of two genes derived from different breeds as in a first cross or F_1 cross.

Other crosses show a proportion of this heterosis equal to ***the proportion of the gene pairs that are heterozygous with respect to breed of origin:***

		one gene pair A A another gene pair A A
Purebreed “A”	Genes from sire:	A A A A A A A A
	Genes from dam:	A A A A A A A A

Heterosis expression = 0%

F_1 cross “A x B”	Genes from sire:	A A A A A A A A
	Genes from dam:	B B B B B B B B

Heterosis expression = 100%

NOTE: This full expression relates to a certain value, such as 25 kg body weight

3 breed cross	Genes from sire:	C C C C C C C C
“C x (A x B)”	Genes from dam:	A B A B A B A B

Heterosis expression = 100%

Back cross	Genes from sire:	A A A A A A A A
“A x (A x B)”	Genes from dam:	A B A B A B A B

Heterosis expression = 50%

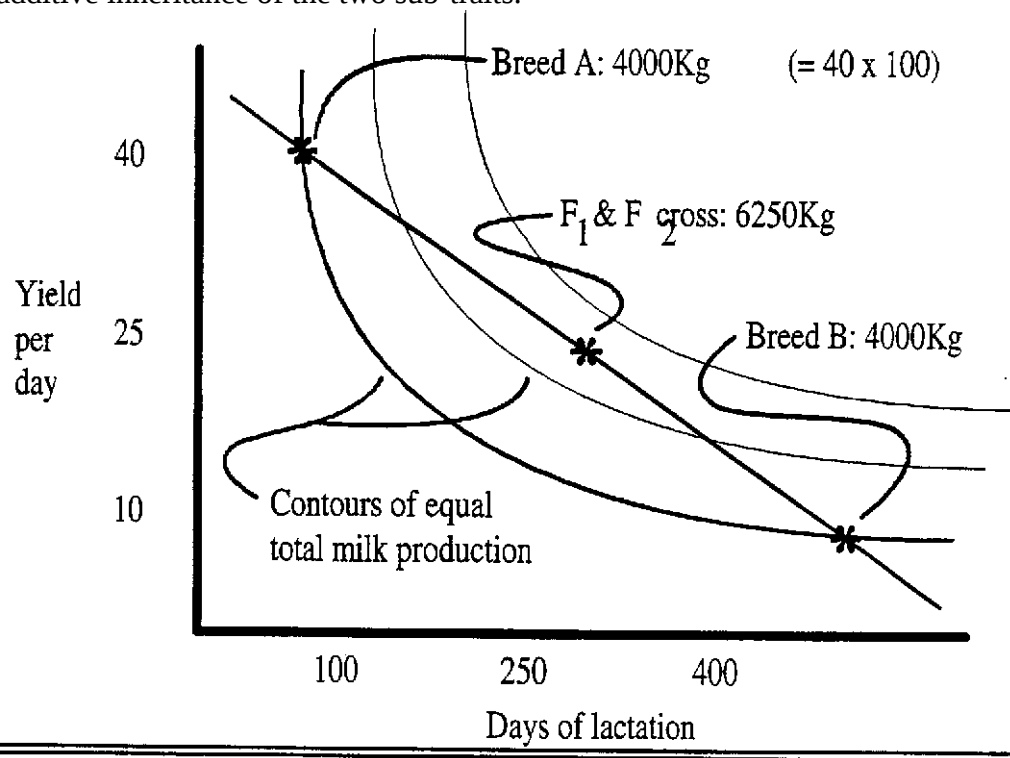
F_2 cross	Genes from sire:	A A B B A A B B
“(AxB) x (AxB)”	Genes from dam:	A B A B A B A B

Heterosis expression = 50%

NOTE: The expression of maternal heterosis can also be calculated in a similar manner, by considering the breed composition of the dam rather than the offspring

Profit heterosis

‘Profit heterosis’ is a theoretical basis for heterosis which does not depend on dominance or epistasis described above. The idealized example here is **milk yield per lactation**, viewed as the product of **yield per day** and **days lactation**. In the graph below, the latter two traits are assumed to have fully additive inheritance, such that the F_1 cross is half way between the parental breeds for these traits. However, due to the multiplicative derivation of the total milk yield, there is notable heterosis in both crosses, with the F_2 expressing as much as the F_1 due to additive inheritance of the two sub-traits.



Profit heterosis could play a role wherever commercially important traits are the multiplicative product of the traits: One possibility is the product of “growth potential” and “environmental tolerance” to give growth in the tropical beef cattle. We generally have little information on this phenomenon, and it is common practice to assume breed **dominance** in the mechanism underlying heterosis.

From here we assume heterosis is caused by dominance- as is common practice.

Systematic crossbreeding systems

Synthetics or composites

These are ‘new breeds’ generated by ‘mixing’ genes from a number of parental breeds. In optimum synthetics, the proportion of genes from each breed is determined in a way that maximizes performance – more use of better breeds improves additive value, but at **some compromise in heterosis expression**.

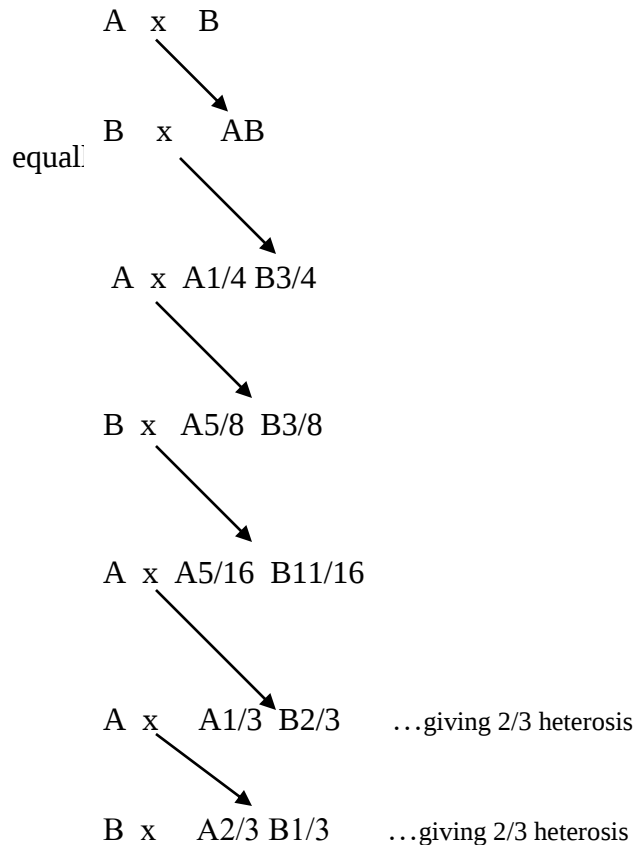
SOME EXAMPLES	
Synthetic	Component breeds
Aust. Milking Zebu	Sahiwal, Red Sindhi
Brangus	Brahman, Angus
Murray Grey	Roan Shorthorn, Angus
Santa Getrudis	Brahman, Shorthorn, others
Polwarth	Merino, Lincoln
Warridale	Border Leicester, Merino
Corriedale	Merino, Lincoln
Kenya Dual Purpose	Toggenburg, Anglo-Nubian,
Goat	Gall and Small East African
Dorper	Dorset, Persian fat- tail

Rotations

Here a different pure breed sire is used each generation, rotating between n breeds. Dams are bred from within the system. The following describes a 2- breed rotation:

PERIODIC ROTATIONS: Here the pattern of rotation gives different emphasis to different breeds. For example: ABACABAC etc. gives more emphasis to breed A. using better breeds more can result in higher genetic merit as with optimum synthetics.

ROTA – TERMINALS: Here a terminal sire is put over a dam which is produced in a rotational crossing programme. If the sire breed is not involved in the rotation, then full direct heterosis is expressed



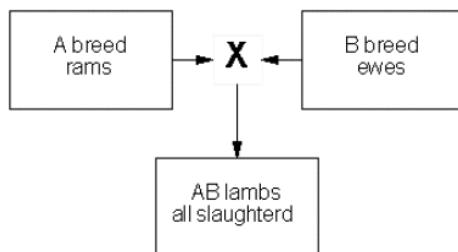
Heterosis expressed in established rotations with n breeds contributing

$$\frac{2^n - 2}{2^n - 1}$$

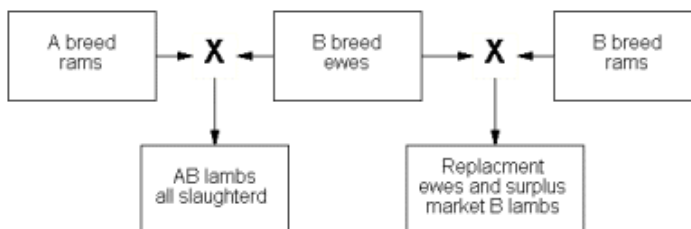
From this it can be shown that rotational crosses express more heterosis than synthetics which use the number of breeds

Examples of crossbreeding systems in sheep

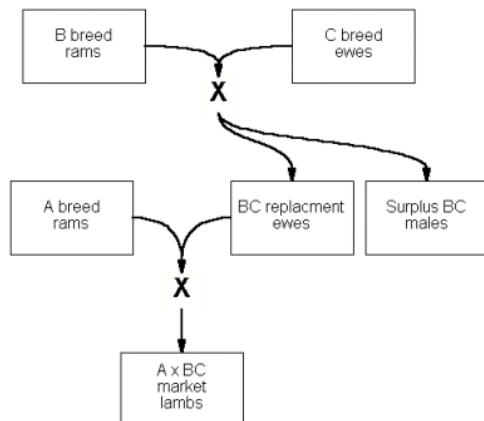
- *Two-breed terminal crossbreeding system*



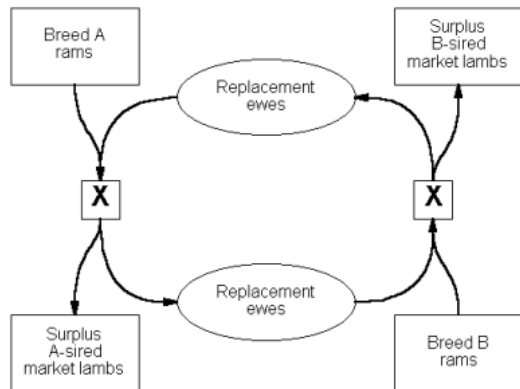
- *Two-breed terminal crossbreeding system with purebred ewe production*



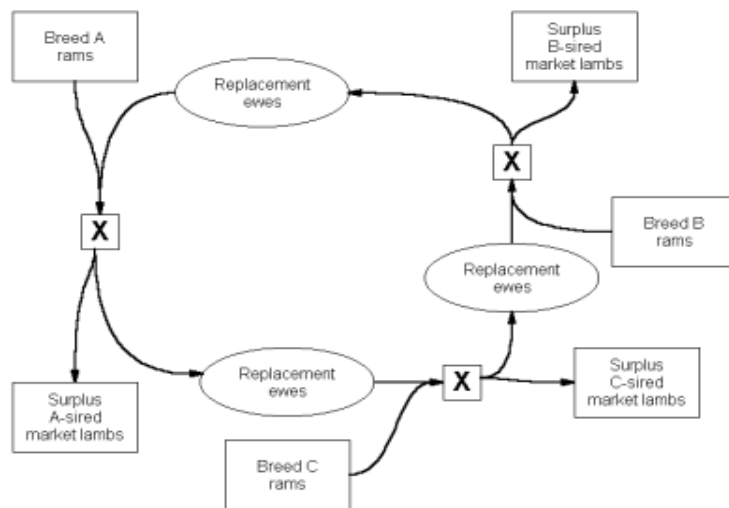
- *Three-bred terminal crossbreeding system*



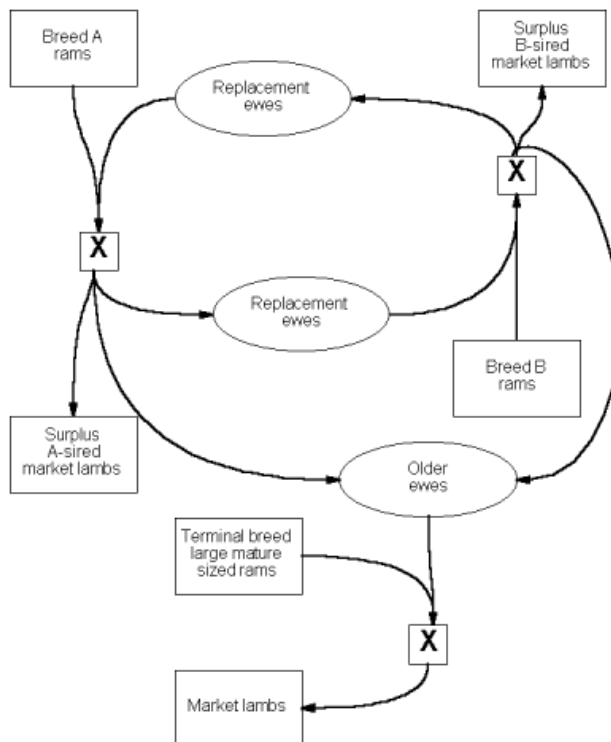
- *Two-breed rotational system*



- *Three-breed rotational system*



- *Three-breed rotational-terminal system*



Which Crossing System to Adopt (If Any)?

PUREBREED	When no cross is better.
F₁ CROSS	When direct heterosis is important.
3 BREED CROSS	When both direct and maternal heterosis are important.
4 BREED CROSS	When paternal heterosis is important as well.
BACKCROSS	When only 2 good parental breeds are available and/or when direct heterosis is not important.
ROTATIONAL CROSSES	When females are too expensive to either buy in or to produce in the same enterprise.
OPEN OR CLOSED SYNTHETICS	When both males and females are too expensive. A few initial well judged importations establish the synthetic (or 'composite'), and it can then either be closed (which helps to establish a breed 'type'), or left open to occasional well judged importations.

The best possible system for maximum **genetic** merit is always a fully structured system, with a short pedigree back to purebreds on both sire and dam sides. E.g. F₁ cross, backcross, 3-breed cross. However, we usually find that such systems are the most **expensive** to run.

Note below the relationship between fecundity and the degree of structure in crossing systems. High fecundity reduces the relative cost of breeding units dedicated to generating crossbred parents, making highly structured systems more viable:

Industry	Fecundity	Typical crossbreeding systems
Poultry	Highest	4- breed crosses
Pigs	Higher	3-breed crosses; backcrosses
Meat sheep	High	3- breed crosses
Wool sheep	Medium	Purebred*
Dairy	Low	Purebred*
Temperate beef	Lower	Rotations; composites
Tropical beef	Lowest	Composites

*Wool sheep and dairy industries are exceptions due to availability of an outstanding pure breed in each.

4. INBREEDING

Introduction

Control of inbreeding is an important aspect of breeding programs. Modern breeding programs have become sophisticated in determining the genetically superior animals. In addition, reproductive technologies such as Artificial Insemination (AI) and Multiple Ovulation Embryo Transfer (MOET) have enhanced the intensive use of the best genetic material. This resulted in obvious gains by a rapid genetic improvement of populations. However, the other side of the coin is that populations become *effectively* smaller, since all the new-born animals descend from only a few highly selected parents. This results in inbreeding, since inbreeding refers to the mating of related parents. If all animals in a population relate to one or only a few 'golden' rams or bulls. Then it will soon be hard to find 'unrelated parents'. Inbreeding and erosion of genetic variation are two phenomena that are closely related.

Definition of inbreeding

INBREEDING – the mating of individuals which are related.

The ***coefficient of inbreeding (F)*** describes the degree of inbreeding in an individual.

F = Probability of the 2 alleles at a randomly chosen locus being ***identical by descent***

Calculation of inbreeding coefficients from pedigree

- Gives exact answers for individuals.

Calculation of the inbreeding coefficients has a similarity with the calculation of the coefficient of Additive Genetic Relationship, which reflect proportion of genes in common between individuals i and j. The probability that an individual has two alleles identical by descent is one half the probability that its parents have alleles in common by descent.

An animal's inbreeding coefficient is one half times the additive genetic relationship between its parents. If individual k has parents i and j, then $F_k = \frac{1}{2} a_{ij}$

Therefore, both F and a_{ij} are calculated in a similar way. Both are calculated by counting steps to a common ancestor.

If we draw a pedigree tree, then the relationship between individuals P and Q can be found by counting the number of steps up (n_1) from P to a common ancestor, and the number of steps down (n_2) from the common ancestor to Q. At each step, the relationship is multiplied by one half, since at each step, there is a chance that a particular allele will not be passed on to an offspring. If P and Q have more ancestors, the relationship is found by summing the probabilities of each of p paths

$$a_{ij} = \sum_{k=1}^p (1/2)^{n_1+n_2}$$

and if animal X is the offspring of I and J, its inbreeding coefficient will be equal to

$$F_x = 1/2 a_{IJ}$$

Example 1

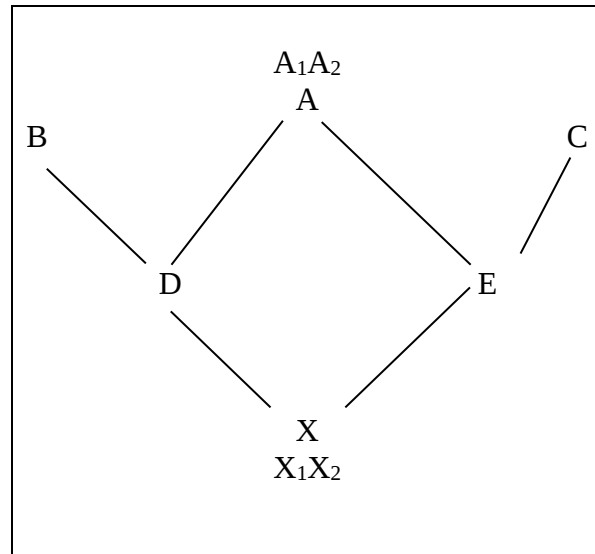
What is the inbreeding coefficient on the offspring of a mating of half sibs?

We can first look at the relationship between D and E. The common ancestor is A, and we have 2 steps ($n_1 = 1$, $n_2 = 1$), and only one path, therefore $a_{DE} = 1/4$ (half sibs). The inbreeding coefficient of X is then $1/2 a_{DE} = 1/8$.

Another (slightly more complicated) way of determining the inbreeding coefficient is to directly derive the probability of two alleles being 'equal by descent':

A_1 and A_2 are the alleles carried by individual A. These are labelled as being different, i.e. not identical by descent, such that A is either known or considered to be not inbred. X's parents (D&E) have a common ancestor (A), and so are related. This means X is inbred.

F = probability that $X_1 = X_2$ by descent – they could either be both A_1 or both A_2 . The chance of X getting A_1 through D is $1/2$ (A to D) times $1/2$ (D to X), and the chance of X getting A_1 through E is $1/2$ (A to E) times $1/2$ (E to X). The argument is similar for A_2 , and so the equation below explains:



$$P(A_1A_2) = (1/2 \times 1/2) \times (1/2 \times 1/2) = 1/16$$

$$F_x = 1/8$$

$$P(A_1A_2) = (1/2 \times 1/2) \times (1/2 \times 1/2) = 1/16$$

And the easiest way to derive F is simply count the number of animals in a loop from an individual to a common ancestor, and back.

Shortcut: $n = 3$ descendants (D, A, E) in the closed loop – $F_x = (1/2)^3 = 1/8$

Example 2:

Inbreeding coefficient on the offspring of a full-sib mating.

Two common ancestors (A & B) of X's parent (C & D) – therefore 2 loops: C <u>A</u> D $(1/2)^3$ C <u>B</u> D $(1/2)^3$ $F_x = (1/2)^3 + (1/2)^3 = 1/4$	
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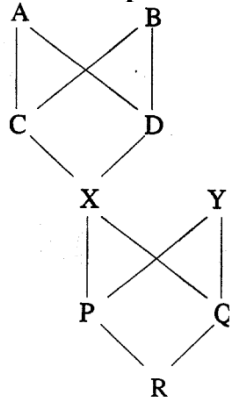
If the **common ancestor is inbred**, there is an increased chance that the two alleles in a descendant will be identical by descent.

Recipe so far is $F_x = \sum (1/2)^n$ where $\sum$ is the sum over loops, and n is the number of animals in each loop, excluding X itself.

BUT – if B in the last example were itself inbred there is a chance (F_B) that $B_1 = B_2$ by descent, and inheritance of B_1B_2 in X contributes to F_x . From this consideration we get the final formula:

$$F_x = \sum [(1/2)^n (1 + F_A)]$$

- where F_A is the inbreeding coefficient of common ancestor A for each loop.
- n is the number of steps in a loop.
- The summation is over all possible loops.

Example 3**Example 3:**

In the pedigree, R results from a full sib mating, but one of the parents is inbred itself

As above, $F_x = 1/4$ (from example 2)

The loops are defined by passing the following animals

P X Q $(1/2)^3 (1+1/4)$ common ancestor X

P Y Q $((1/2)^3 (1+0))$ common ancestor Y

And the resulting inbreeding coefficient is $F_R = 9/32 = 0.28125$

Further Remarks about inbreeding coefficient

Ultimately all individuals in a population might find themselves somehow related to each other. One might even argue that every locus that is homozygous carries two alleles that are somehow identical by descend, because they have to relate to the original mutation. Practically, we can never write down a pedigree to ancestors of every generation ago. Therefore, the inbreeding coefficient tells us how much more probability there is that genes are in common, relative to a certain base population (practically, the first ancestors in the pedigree). If the allele frequency in the base population is p , the probability that two alleles are identical in a random animal of a base population is p^2 . However, the probability that an inbred descendant carries the same alleles would be increased.

We can therefore summarize the following consequences

- The inbreeding coefficient is relative (to a base population). We usually talk about F (rate of inbreeding (increase) rather than an (absolute) value at a current time.
- Inbreeding is also not attempting to measure degree of homozygosity. Although homozygotes are increased with inbreeding, there is also homozygosity by randomness.
- Inbreeding does not change gene frequencies, only genotype frequencies

Deviations from Hardy Weinberg in an inbred population (for single locus –2 allele model)

Genotype	HW-equilibrium (Non-inbred)	Inbred population
A_1A_1	p^2	$p^2 + pqF$
A_1A_2	$2pq$	$2pq(1-F)$
A_2A_2	q^2	$q^2 + pqF$
Allele Frequency A_1	p	p

An individual with an inbreeding coefficient F has therefore F % less heterozygosity.

In the following paragraph we see that this has negative consequences, for example in case of genetic defects.

- Inbreeding is temporarily. It is a configuration of genotype frequencies that typically has more homozygotes (of either kind). However, as soon as different inbred strains cross, the inbreeding is completely disappeared.
- Of course, if we had no 'other' lines, an inbred populations might fix its genes due to drift (or due to selection if selected), thereby losing its genetic variation. In that case, inbreeding is not so temporarily.

Consequences of Inbreeding: Why is inbreeding bad?

1) Increased frequency of affected individuals due to genetic defects'

Inbreeding increases the frequency of homozygotes. This is a disadvantage, since many mutations that occur have a negative effect, but luckily they are usually recessive (otherwise they

might not have survived). The effect of deleterious recessive alleles comes only to expression in homozygotes (carrying two copies of the recessive allele).

This is applicable to genetic defects, which are usually due to recessive alleles in small frequencies. If the frequency of the recessive allele is q , then in a non-inbred population, the probability of being an affected individual is q^2 . An inbred individual would have a probability of $q^2 + pqF$.

Let q be equal to 1 %. We have then

	<u>Probability of being affected</u>
Normal individual:	1 in 10,000
Inbred individual ($F=0.125$)	13.4 in 10,000
Hence a large increase!	

2) *Inbreeding depression*

The effect of increased frequencies of individuals that are homozygous for negative recessive effects translates for quantitative traits, regulated by possibly many genes, into inbreeding depression. Increased homozygosity means most traits are depressed by between 2% and 7% per 10% increase in F . Since we observe the phenomena only for alleles that are recessive, we should observe inbreeding depression only for traits that show dominance. Those are typically traits that relate to *fitness and reproduction*.

Inbreeding depression is a 'mirror image' of heterosis, the first is due to a shortage of heterozygotes, the second due to an excess of heterozygotes. Heterosis if more distant line or breeds are crossed (as we saw under crossbreeding) We will find a lot of heterosis for the same traits that show a lot of inbreeding depression.

3) *Inbreeding leads to a loss of genetic variance.*

The variance in an inbred population will decrease, because the animals become increasingly related and therefore more and more 'alike', hence less variation within the population. A loss of variation due to inbreeding hampers the genetic improvement that potentially can be made. For a long term genetic response, it is therefore important to keep inbreeding below a certain level.

5. NUCLEUS BREEDING SYSTEMS

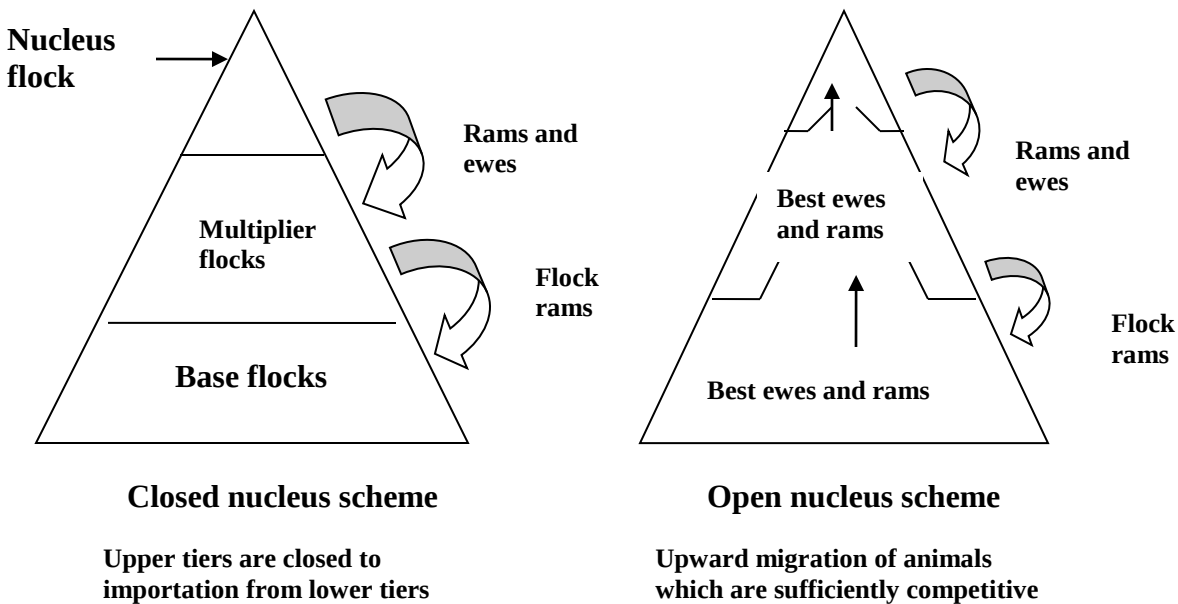
Given a breeding objective, all the breeding programmes are driven by decisions on:

- *how to allocate measurement effort*
- *which animals to use for breeding*
- *how to allocate mates*

Mates can be allocated across flocks (or herds etc.) and breeds, as well as within flocks.

Nucleus Breeding Systems and Breeding Pyramids

An industry can contain millions of animals. It is not worth including them all in a breeding program due to measurement costs, recording costs, and lack of proper control. The solution is to concentrate efforts on relatively few elite breeding units (nuclei) at the top of a pyramid structure, and disseminate the superiority to the whole industry (Figure 1)



Closed nucleus breeding schemes

Closed nucleus schemes are closed in that no breeding stock are imported into the top level. In reality, there is usually a fair bit of migration between different flocks and herds in the top one or two tiers. Closed schemes have evolved in most animal industries driven largely by market forces. Here are some key properties of closed schemes:

1. Selection effort is only permanently effective in the nucleus- any temporary changes in the lower tiers are diluted by importation from the nucleus (Figure2).
2. Nucleus breeding objectives impact on the whole scheme.
3. If lower tiers buy from the average rams (and no ewes) from the tiers above, they will lag behind the tier above by 2 generations (about 7 years in sheep) of selection response (Bichard, 1971).

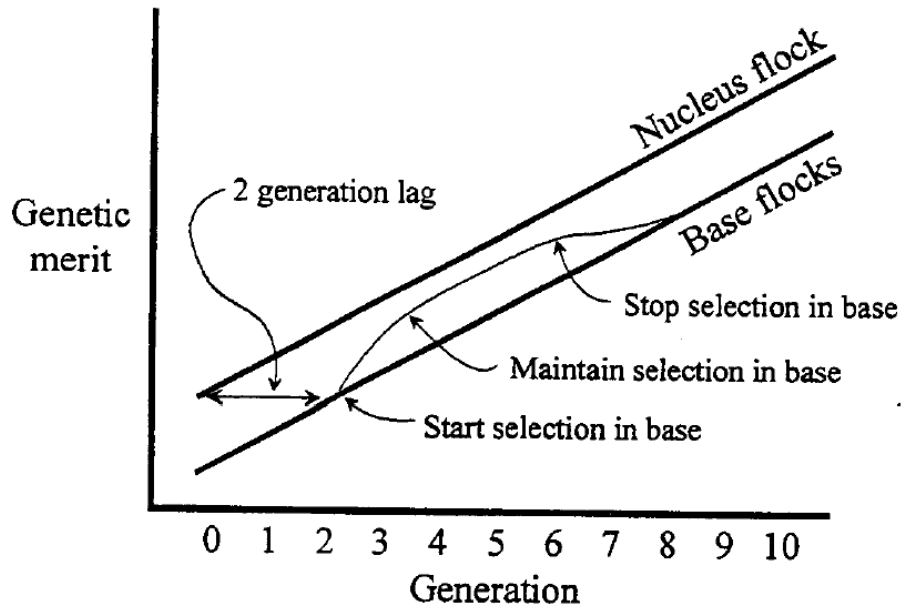


Figure 2. Selection response in a 2-tier closed nucleus scheme. The base lags about 2 generations behind the nucleus. Any selection effort in the base needs to be maintained just to keep a non-increasing advantage. Opening the nucleus will give more sustained returns from selection in the base.

Open nucleus breeding schemes

Stock in the base tier(s) can have higher EBV's than nucleus stock that would have otherwise been selected. This is most true for animals of low fecundity, such as ewes.

These high-merit base ewes can be migrated up to be bred in the nucleus, giving an open nucleus scheme. This pushes the nucleus to progress more quickly and this benefits the whole scheme as the base will move as fast as the nucleus after things have settled down. Overall response in open 2-tier schemes is 10 – 15 % faster than in closed schemes when optimal design is applied: about 10% of the population in the nucleus and about 50% of nucleus mated ewes born in the base (James, 1977).

Why do open nucleus schemes perform better?

Use the best stock to make an elite nucleus move quickly, then let the rest of the population enjoy the benefits. There can be some increased lag between the tiers, but this is compensated for quite quickly.

However this can be viewed from a different angle. Assortative mating (mating best to best) gives extra response due to increased genetic variation in the next generation. We could simply do this across the whole population, but the open nucleus system does it at just two or three levels (tiers), with generally random mating within tiers. However, the open nucleus design has an added advantage- knowing the source of an animal (the tier of its birth) tells us something about its likely genetic merit even if we do not know its pedigree or its measurements:

Because each tier contains many animals, tier means for given traits constitute high quality information – they are highly heritable. In simple nucleus schemes we measure animal merit as deviations from flock mean (regressed by heritability, as in chapter 6).

If we add this to the flock- of-birth genetic means we get simple estimates of across-the flock EBV's. This flock mean is like the mean of a big family. Thus, in the absence of normal pedigree information, we get an added boost in overall selection accuracy through use of this crude but effective “family” information.

This extra information about genetic merit is essentially redundant in the effect of full pedigree information. This means that we could capture all the benefits of an open nucleus scheme by using the pedigree information to select on BLUP EBVs, and mating assortatively. In this case there would be no need to migrate ewes-as long as we could generate all desired matings by migrating semen between flocks.

Geographically diffused nucleus schemes

As suggested in the last section, we can enjoy the full benefits of an open nucleus scheme without nominating one flock or herd to be the nucleus. We can create the elite ‘nucleus’ mating in the herds of birth of female partners, with migration of semen to these herds. This relies on good pedigree information without which lack the useful information about the tier of birth that a simple open nucleus scheme manages to exploit.

Geographically diffused nucleus schemes are in fact very common. The classical four-pathway dairy breeding design, is in fact a geographically diffused nucleus design.

Design of dairy breeding programs

Dairy breeding programs are a somewhat special case in the design of breeding programs as they have a 4- pathway structure. Also the dairy industry is relatively advanced in taking up new technologies, such as use of EBVs, A.I and other reproductive technologies. It is therefore an interesting case to study when it comes to the effect of new technologies on breeding program design.

Worldwide dairy breeding is characterised by

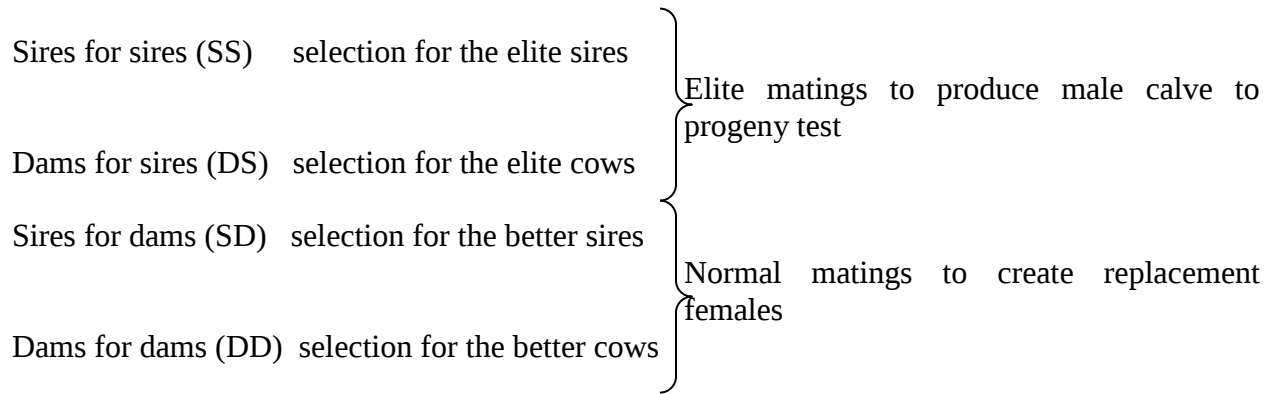
- -high degree of data recording, about 70% of commercial farms participate in milk recording schemes.
- -Widespread use of A.I, high proportion of calves are born through A.I.

The combination of widespread herd recording and A.I, i.e. using sires across many herds, provides a good structure for genetic evaluation. EBV's of both bulls and cows are comparable over different herds. Of all livestock industries, the use of information provided by EBVs is mostly accepted in dairy.

A typical feature of the design of a dairy breeding program is the 4-pathway breeding structure. The two main reasons for a special design is that:-

- -many more females are needed for breeding than males.
- -males are selected based on a progeny test, as males don't produce themselves, but an accurate EBV is needed before they can be used widely.

Progeny testing is expensive and obviously not all males born in the dairy population are tested. Only males that are offspring of the very best progeny tested sires will be selected as young bulls for progeny testing. On the other hand, most of the newborn females are needed as replacement and their parents cannot be so highly selected. The 4 path way selection structure consists now of the following pathways:



6. APPLICATION OF MOLECULAR GENETICS IN ANIMAL BREEDING: GENE MAPPING, GENETIC MARKER ASSISTED SELECTION

Quantitative genetics uses phenotypic information to help identify animals with good genes. Molecular genetics techniques aim to locate and exploit gene loci which have a major effect on quantitative traits (hence QTL - Quantitative Trait Loci).

Introduction

Most livestock industries successfully developed EBV's to allow identification of the best breeding animals. EBVs are best calculated using BLUP, meaning that they are based on performance information of several traits from the individual animal and its relatives. Selection based on BLUP-EBVs is currently the most accurate method to select genetically superior animals based on performance recording.

Although the idea of genetic selection is to improve the genes in our breeding animals, we actually never really observe those genes. Selection is based on the final effect of all genes working together, resulting in the performance traits that we observe in the production animals. The strategy makes sense, since we select based on what we actually want to improve. However, animal performance is not only affected by genes, but also by other factors that we do not control. For this, reason selection for the best genes based on animal performance alone can never reach perfect 100% accuracy. A large progeny test comes close such a figure of perfect selection. But this is expensive for some traits (e.g. for traits related to carcass quality), and we have to wait several years before progeny test can be used.

Successful breeding programs are characterised by selecting animal at a young age, leading to short generation intervals and faster genetic improvement per year. For selecting at younger ages, knowledge about the existence of potentially very good genes could be very helpful.

Quantitative trait loci (QTL)

Quantitative genetics uses phenotypic information to help identify animals with good genes. Molecular genetics techniques aim to locate and exploit genes, which have a major effect on quantitative traits (hence QTL - Quantitative trait loci). Identification of the individual genes could lead to several useful applications:

1. It could improve the efficacy of selective breeding, especially for traits with low heritability or that can only be measured in one sex.
2. Transgenic technology might be applied to quantitative traits.
3. In medicine, the identification of alleles causing predisposition to common multifactorial disease, such as heart disease or diabetes, could lead to improved methods of prevention.
4. Quantitative genetic theory will be made more realistic when the numbers and properties of the genes are known and the more realistic theories will improve our understanding of evolution.

With so many mapped markers it is now possible to find QTL (*REFER TO QUANTITATIVE GENETICS NOTES FOR already known to exist and how to search for unknown QTL*). There are two types of 'gene searching'.

Marker assisted selection (MAS)

The idea behind marker assisted selection is that there may be genes with significant effects that may be targeted specifically in selection. Some traits are controlled by single genes (e.g. hair colour) but most traits of economic importance are quantitative traits that most likely are controlled by a fairly large number of genes. However, some of these genes might have a larger effect. Such genes can be called major genes located at QTLs. Although the term QTL strictly applies to genes of any effect, in practice it refers only to major genes, as only those will be large enough to be detected and mapped. Following the inheritance at such QTL might assist in selection.

Types of Markers

Direct markers

The easy scenario is when the marker allele M and the QTL-allele G are always together. This is only the case if the marker is actually measuring the relevant polymorphism within the gene that causes the effect. Such a *direct marker* is very convenient, because the marker genotype will directly inform us about the QTL genotype. However, there are currently only a few direct genetic markers for economically important traits.

Linked markers

Linked markers require some ongoing activity in trait measurement and pedigree recording which makes them less appealing than direct markers. Linked markers are only near and not on top of a QTL on the genome. For a randomly chosen animal in the population, we have no clue whether one or another marker allele is associated with a preferable QTL allele. If we observe within the progeny of one sire a difference in between different marker alleles (as M and m in the figure above) we can determine which of the marker alleles is associated with the preferred QTL allele. But this information is only useful for this particular sire, and its family!

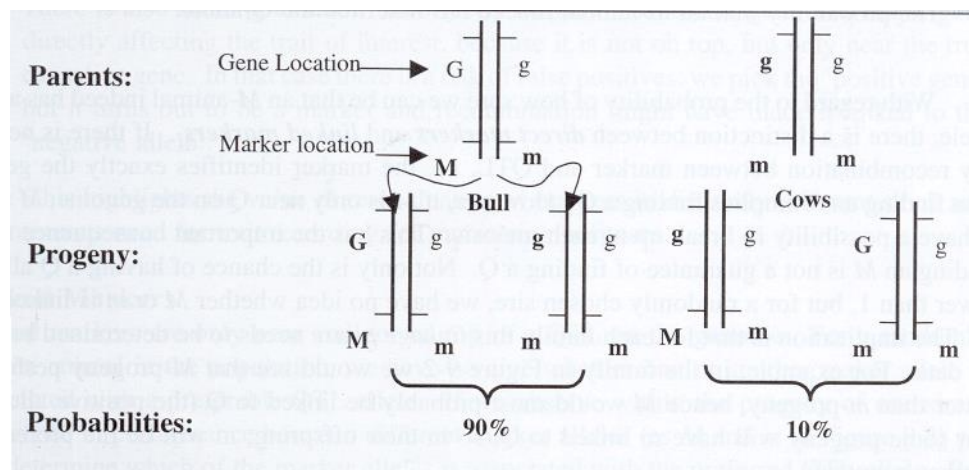
With linked markers, the information on which marker genotype is linked to the positive QTL allele is family specific. This linkage phase has to be determined by genotyping at least 2 generation (a sire and its progeny), and using phenotypic information on the progeny. In addition, it will in most cases be useful to also genotype dams, since otherwise it will be unclear which marker allele an animal received from its sire. In a number of families we can detect linkage, because the sires are homozygous, either for the marker or the QTL.

It may be obvious that there is a considerable need to gather trait and pedigree information for use of linked genetic markers because for each family the linkage phase between marker and QTL needs to be established. However, many breeding populations already have a performance and pedigree recording system in place. Furthermore, the need for large half-sib families is also reduced over time, as marker and trait information is gathered on a deeper pedigree. This is because we now have methods to use information from all relatives to make inference about which marker variant is linked to the superior gene variants in each animal. Once a linkage phase has been established for a family, as is the case for a tested sire, trait measurement is not required for additional progeny of that sire.

Indirect markers need continuous trait recording and a lot more genotyping compared to direct markers. In spite of this, the genotype of animals for specific genes cannot be given with

certainty in the case of indirect markers. This may give marketing problems compared to the use of a direct marker test, which can nearly guarantee small difference in expected prediction with the use of marker haplotypes in the context of performance and pedigree information available for nucleus animals.

When making selection decisions based on marker genotypes, it is important to know what information is exactly contained by the marker genotype. The figure below shows the principle of inheritance of a marker and a linked QTL. We can identify the marker genotype (Mm) but not the QTL (Gg). The last is really what we want to know because of its effect on economically important traits.



Let the G allele have a positive effect, therefore being the preferred allele. In the example, the M marker allele is linked to the G in the sire. Progeny that receive the M allele from the sire, have a high chance of having also received the G allele, and are therefore the preferred candidates in selection.

As shown in the figure above, there are 4 types of progeny. All progeny will inherit m alleles and g alleles from the mother. The sire will provide them with either an M- or an m- allele and either G or g. In the figure, 90% of the progeny that receives an M-allele have also received a G-allele, because M and G alleles are linked on the same chromosome in the sire. However, in 10% of the cases while the sire produces gametes, there will be a *recombination* between the two loci, and animals that inherited an M-allele from the father have received a g-allele rather than a G-allele. Marker alleles therefore do not always provide certainty out the genotype at the relevant QTL.

Animals may be selected based on the marker information only. This is a good idea only if the marker is linked to a single gene causing all of the genetic variation. Usually we imagine that there may be a major gene/QTL, but there are many other important genes, not covered by the marker. In that case we want to combine the information on markers with information on phenotype. The first aims to get the good QTL, the second aims at getting also good 'other genes'. Selection with the aid of information at genetic markers is termed marker assisted selection (MAS).

Selecting for QTL genotypes

Where a direct marker (DNA-test) exists for a QTL, we can use Genotype Assisted Selection (GAS). Where only linked markers exist for a QTL, we must use Marker Assisted Selection (MAS). In either case, the aim is to determine QTL genotypes to assist selection decisions, either to increasing the frequency of favourable QTL alleles, or targeting their introgression into other lines. The value of this depends on a number of factors:

- Where heritability is low, the value of information on individual QTL tends to be higher because accuracy of breeding values is relatively more increased.
- Where the trait(s) of interest cannot be measured on one sex, marker information gives a basis to rank animals of that sex.
- If the trait is not measurable before sexual maturity, marker information can be used to select at a juvenile stage.
- If a trait is difficult to measure or requires sacrifice (as with many carcass traits) marker information can be used instead.

ANIMAL BREEDING IS ENDLESS, DISCOVER MORE AS YOU CONTINUE READING, MINE WAS TO STIR YOUR INTEREST, I HOPE I HAVE!!! BE BLESSED