

COURSE CODE:	ABG 500
COURSE TITLE:	APPLIED ANIMAL BREEDING AND GENE
NUMBER OF UNITS:	3 Units
COURSE DURATION:	Three hours per week

COURSE DETAILS:

Course Coordinator:	Prof. M. O. Ozoje, (<i>B. Sc., M. Sc., Ph.D., MNSAP, MASAN, MGSN</i>)
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COURSE CONTENT:

Variances, Co-variances, Partitioning of phenotypic variance, Heritability and repeatability, Genotype by environment interaction, Correlation between traits, In-breeding, Line breeding and relationship, Cross-breeding in practice, selection in practice, Genetic improvement for various livestock traits.

COURSE REQUIREMENTS:

This is a compulsory course for all students in the College of Animal Science and Livestock Production. In view of this, students are expected to participate in all the lectures and practical and must meet up with a minimum of 75% attendance to qualify for the final examination.

READING LIST:

Quantitative Genetics by J. P. Jain

Understanding Animal Breeding by Goudon

LECTURE NOTES

Variation

The examination of most animal species reveals the existence of phenotype difference between individuals for example in cattle there are obvious difference in coat colours and the presence and absence of horns. If cattle are weighed or if milk production is recorded there will be difference in performance between individuals. These differences between individuals of the same species or breed for the same trait or character is called Variation. This may be classified into two or more categories depending on the character examined and upon the unit of measurement used.

Those character for which there are two or only relatively distinct categories are described as showing discrete variation. For other characters where the number of categories is large and limited to the units and accuracy of measurement used for classification, these characters are described as showing continuous variation. Discrete and continuous variations are the extremes of a scale of variation which can be found by investigating a number of characters.

Variation among animals in size, rate of growth, efficiency of feed utilisation, carcass characteristics, disease resistance etc has been observed.

Both heredity and environment are important in producing difference among individual animals. In some instances, there are specific hereditary and environmental influences that may produce variability which is not directly attributable to either but which is a result of their joint action or interaction. The majority of characters of interest in animal breeding are continuously varying in the sense that individuals cannot be readily classified into distinct classes. Continuously varying characters are quantitative characters or metric characters. Milk production, fleece weight, body weight and the various linear measurement traits are examples of continuously varying characters. Continuously varying characters are called quantitative characters or metric characters. The measurement of the variation in a trait or character is called variance, which can be divided into different components.

Causes of Variation

Traits generally are grouped into those which show qualitative differences and those which show quantitative difference. In the former, the variation fall into a few clearly defined classes which is usually due to the fact that these traits are under the control of one or a few pairs of genes whose final expression is not greatly influenced by external environmental factors. The polled or horn consideration in cattle is an example of qualitative traits. On the other hand the variation from small to large as are found in milk production and rate of gain is an example of quantitative variation.

The study of variation consists of two stages. The first is a description of the phenotypic variation. The second is a translation of these phenotypes into genetic terms and the re-description of the variation genetically. Variation among phenotypes in a population arises from three sources. First is the average difference between genotypes, the second is the variation from environmental source and thirdly, the Interactions between heredity and Environment.

Phenotypic variation refers to the observable or measurable difference among individuals within a population for a particular trait.

1. Genetic Source of Variation: A measure of genetic variation is the amount of heterozygosity at a locus in a population which is given by the total frequency of heterozygotes at a locus. The genotype of an individual is fixed at conception and barring a mutation remains the same for the remainder of its life. Its genetic makeup is determined by the genes that it receives from both parents.

The individual as well as its parent possess thousand of genes. Members of an inbred animals are more likely to be alike genetically than non inbred individuals. The degree of genetic similarity among individuals within an inbred line increases as the amount of inbreeding increases especially if there is directional selection.

Parents homozygote for many pairs of genes will have more offspring that are more alike genetically than parents that are heterozygous for several of genes. In fact genetic variability within a species is almost unlimited.

Environment Source

Phenotypic variations in economic traits due to environment are also of great importance.

The environmental portion of the phenotypic variation may be denoted by the symbol σ^2_e . Environment includes all such factors as disease nutrient supply, temperature effects accident and others which the individual may encounter from the time of conception until its death.

Phenotype variations due to environment are important because 1. They are not transmitted from parents to their offspring, 2. They overshadow variation due to heredity. 3. the proper environment is necessary for an individual to reach its genetic potential and 4. rapid improvement can be made in the efficiency of livestock production by supplying uniform and superior environmental conditions to breeding animals.

3. Interactions between heredity and Environment

The interaction between heredity and environment means that animals of a certain genotype may perform more satisfactorily in some environment than in another. In other words one environment permits the expression of the genetic characters in a breed or strain another does not.

Variance

The amount of variation is measured and expressed as the variance when values are expressed as deviation from the population mean. The variance is usually denoted by σ^2 and is defined as the average of the squared deviations from the mean. It is the most useful measure of variation for studying the variability of population.

Variation among phenotypes in a population arises majorly from two sources. First is the average difference between genotypes and the second is the variation from environmental source. The total phenotypic variance of a population (S_P^2), i.e. the measure of the observable variation, can be broken into two portions; the variance among genotypic means (S_G^2) and the remaining variance often classified as the variance due to environmental deviations (S_E^2). The former is called genetic variance and the latter is environmental variance. The breakdown of the phenotypic variance into the sum of environment and genetic values lives out the possibility of some covariance between genotype and environment. If the phenotype is the sum of genetic and an environmental effect, then $P = G + E$. If the genotypes are not distributed randomly across environment, there will be some covariance between genotype and environmental values and the covariance will be hidden in the genetics and environment variance.

$$S_P^2 = S_G^2 + S_E^2 + 2 \text{ covge}$$

The measure of genetic influence tell us the portion of the population variation in phenotype that can be assigned to variation in genotype. It does not tell us the portions of an individual phenotype that can be ascribe to its heredity and its environment. All measures of importance of genes are framed in terms of the proportion of variance ascribable to their variations. The basic idea in this study of variation is the partitioning of total phenotypic variation into the components attributable to different causes. The relative magnitudes of these components determine the genetic proportion of the population and the degree of resemblance between relatives.

VARIANCE COMPONENT

The amount of variation is measured and expressed as the variance in a trait or character. When values are expressed as deviation from the population means, the variance is simply the mean of the square values of the deviations. The components into which the variance is partitioned are the genotypic variance or variance of genotypic values and the environmental variance or variance of the environmental deviations. The total variance is the phenotypic variance or the variance of phenotypic values and it is the sum of the separate components. The total variance, therefore, with certain qualifications, can be expressed as $V_P = V_G + V_E$, which is the same as $V_A + V_D + V_I + V_E$ in which case, V_P will be increase by twice the covariance of G and E. (2). There may be interaction between genotype and environment, in which case, there will be an additional component of variance attributable to interaction.

The partitioning of the variance into its components allows one to estimate the relative importance of the various determinants of the phenotype. The relative importance of a source of variation is the importance of heredity in determining phenotypic value is called the heritability of the character. The ratio V_g/V_p expresses the extent to which an individual phenotype is determined by the genotype. It generally expresses heritability in the broad sense i.e. the degree of genetic determination.

The ratio V_A/V_P expresses the extent to which phenotypes are determined by the genes transmitted from the parents. It determines the degree of resemblance between relatives and is therefore the greater importance in breeding programs.

Estimation of the genotypic variance V_g is simple in theory, but difficult in practice. Neither the genotypic nor the environmental components of variance can be estimated directly from the observation of a single population measure, but in certain circumstance, they can be estimated in experimental population.

GENETIC COMPONENT OF VARIANCE

The partitioning of total variance into genotypic and environmental variance does not take us far in the understanding of the genetic properties of a population and in particular, it does not reveal the cause of resemblance between relatives. The genetic variance must therefore be further partitioned or subdivided according to the division of genotypic values into breeding values (Additive gene effect), dominance deviation and interaction deviation, thus: the value $G = A + D + I$ and the variance components $V_G = V_A + V_D + V_I$. The additive variance, which is the variance of breeding value, is the important component since it is the chief cause of the resemblance between relatives and therefore the chief determinant of the observable genetic properties of the population and of the response of the population of selection. In

practice therefore, the important partitioning is into additive genetic variance versus all the rest, i.e. non-additive genetic and environmental variance. This partitioning yield the ratio V_A/V_P which is the heritability of the character. Estimation of the additive variance rest on the observation of the degree of resemblance between relative.

ENVIRONMENTAL VARIANCE

Environmental variance by definition embraces all variation of non-genetic origin can have a great variety of causes and its nature depends very much on the character and the organism studied. Environmental variance is a source of error that reduces precision in all genetic studies and the aim of the breeder is therefore to reduce it as much as possible by careful management or proper design of the experiment. Nutrition and climatic factors are the commonest external causes of environmental variation and they are at least partly under experimental control. Material effects form another source of environment variation that is sometimes important, particularly in mammals but is less susceptible to control. They are pre and postnatal influence, mainly nutrition of the mother on the young.

HERITABILITY

Heritability can be defined as the proportion of total variance that is due to genetic variance.

$$h^2 = V_g^2/V_p^2 = V_g^2/V_g^2 + V_e^2$$

Heritability so defined is called broad h^2 of the character. It must be stressed that the measure of genetic influence tells us what portion of the population variation in phenotype can be assigned the variation in genotype. An individual phenotype is a consequence of the interaction between its genes and its environment.

The heritability of a character is one of its most important properties. It expresses the proportion of the total variance that is attributable to the average effect of genes, and this is what determines the degrees of resemblance between relatives. But the most important function of the h^2 in the genetic study of metric character is its predictive role, expressing the reliability of the phenotypic value as a guide to the breeding value. Only the phenotype of ht individual can be directly measured, but it is the breeding value that determines their influence their influence in the next generation. Therefore if a breeder chooses an individual to be parent according to their phenotypic values, his success in changing the characteristics of the population can be predicted only from a knowledge of the degree of correspondence between phenotypic values and breeding values. This degree of correspondence is measured by the heritability. In other words, heritability expresses the reliability of the phenotypic value as a guide to the breeding value, or the degree of correspondence between phenotypic

value and breeding value. For this reason heritability enters into almost every formula connected with breeding methods and many practical decisions about procedures depends on its magnitude.

ESTIMATION OF HERITABILITY

Heritability is estimated from the degree of resemblance between relatives. The choice of what sort of relatives to us for the estimation depends on the circumstances. In addition, precision and bias are other points to be considered. The closer the relationship, the more precise the estimates. Generally speaking the half sib correlation and regression of offspring on father are the most reliable. The regression of offspring on mother is sometimes liable to give too high estimate on account of maternal effects. The full sib correlation is the least reliable of all. The component due to common environment is often present in large amount and is difficult to overcome by experimental design and full sib covariance in further augmented by the dominance variance.

OFFSPRING – PARENT REGRESSION

The estimation of heritability from the regression of offspring on parents is comparatively straightforward. The data are obtained in the form of measurement of parents. – one or mean of both-and the mean of their offspring. The covariance is then computed from the cross products of the paired values. The following example illustrates the regression of offspring on paternal values. A complication in the use of the regression of offspring on parent arises if the variance is not equal in the two sexes.

The statistical model is $Z_i = \beta X_i + e_i$ where Z_i is the mean of the offspring of th I-th sire. X is the observation on the I-th sire, β is the regression of Z on X and e_i is the error associated with Z 's.

Computational formulas

1. Obtain ΣX^2 , ΣY^2 and ΣXY

$$\Sigma X^2 = \Sigma X^2 - \frac{(\Sigma X)^2}{N}$$

$$\Sigma Y^2 = \Sigma Y^2 - \frac{(\Sigma Y)^2}{N}$$

$$\Sigma XY = \Sigma XY - \frac{(\Sigma X)(\Sigma Y)}{N}$$

Where N is the number of parent -offspring pair

$$b = \frac{\sum XY}{\sum X^2}$$

2. Heritability (h^2) = 2b

3. Standard error

$$\text{(Variance) } S_b^2 = \frac{\sum Y^2 - \frac{(\sum XY)^2}{N}}{\sum X^2 - N}$$

$$\text{S.E. (b)} = \sqrt{\frac{S_b^2}{\sum X^2}}$$

$$\text{S.E (} h^2 \text{)} = 2 \text{ S.E. (b)}$$

Example: A reference population consist of a large non-inbred flock of Yankassa. Individuals were weighed at 16 weeks to the nearest KG. When matured, seventeen males were randomly selected and mated and their male progeny weighed at 16 weeks. The sire weight and the mean weight of their male progenies are as given below. Estimate the heritability of 16th week weight.

Sire weight (X) 6.01, 7.33, 7.93, 7.95, 8.18, 8.38, 8.54, 8.8, 8.82, 8.95, 9.52, 9.53, 9.61, 9.79, 9.95, 9.97, 10.40

Progeny weight (Y) 9.1, 9.83, 9.76, 10.5, 10.8, 10.4, 10.4, 10.25, 9.94, 10.30, 10.21, 10.78, 9.64, 9.76, 11.10, 10.41, 10.35

SIB ANALYSIS

The estimation of heritability from half sibs is more complicated than it appears at first sight. A common form in which data are obtained with animals is the following. A number of males (sires) are each mated to several females (dams), the males and females being randomly chosen and randomly mated. A number of offspring from each female are measured to provide the data. The individuals measured thus form a population of half sibs and full sibs

families. An analysis of variance is then made by which the phenotypic variance is divided into observational components attributable to differences between the progeny of different males (the between sire component, (σ_s^2) , to differences between the progeny of female mated to the same male (between-dam, within sire components, σ_d^2); and to difference between individual offspring of the same female (within progenies components, σ_w^2). They are supposed to be S sires each mated to D dam, which produce K offspring each. The values of the mean squares are denoted as MSS, MSD and MSW. The mean square within progenies is itself the estimate of the within-progeny variance component, σ_w^2 , but the other mean squares are not the variance components. The between-dam mean square, for example is made up of the within progeny component together with the K times the between-dam components, so the between-dam component is estimated as:

$$\sigma_d^2 = (1/k) (MSD - MSW),$$

Similarly, the between sire component is estimated as:

$\sigma_s^2 = (1/p) (MSS - MSD)$, where p is the number of offspring per sire. If there was unequal number of offspring, from the dams, or of dams in the sire groups, the mean values of K and D can be used with little error, provided the inequality of numbers is not very great.

Source	df	Means square	Composition of mean squares
Between sires	S - 1	MSS	$\sigma_w^2 + k \sigma_d^2 + dk \sigma_s^2$
Between dams (within sires)	D - S	MSD	$\sigma_w^2 + k \sigma_d^2$
Within progenies	sd (k-1) or N - D	MSW	σ_w^2

Example 1. (no dam effect)

The reference population was a large non-inbred flock of goats. twenty sires were chosen at random, each sire mated to eight dams with each mating producing one male. Five sire families were chosen at random and progeny 12 weeks body weight in kg obtained. Estimate sire, progeny components of variances and heritability of body weight at 12 weeks.

SIRES

A	B	C	D	E
6.87	6.18	6.18	6.00	7.17
6.91	6.80	6.87	6.57	6.58
7.93	5.92	7.63	6.69	6.74
6.75	6.83	7.47	6.06	6.11
7.00	6.31	6.78	7.18	6.78
7.53	6.91	7.37	6.93	7.88
7.04	6.94	7.31	6.69	6.50
7.17	7.32	6.03	6.48	6.90
57.2	53.21	55.64	52.60	54.66

Compute the Analysis of variance like CRD and get the MS. But note, there is a difference in Df. See the table above. SS_{error} is estimated as $SS_{\text{total}} - \text{uncorrected } SS_{\text{sire}}$ not correction factor. The estimate the variance components from the MS as shown above. E.g $\sigma_s^2 = (I/p) (MSS - MSD)$. The mean square within or error is itself the estimate of the within variance component, σ_w^2

Standard error of heritability is estimated as $4 \sqrt{\frac{2(1-t)^2 [1 + (k-1)t]^2}{k(k-1)(s-1)}}$ Where

$$t = \frac{\sigma_s^2}{\sigma_s^2 + \sigma_w^2}$$

Example 2:

Determine the heritability of weight in kg for test boars at eight weeks of age of six sires which had been mated to three dams each; three sons were weighed at weaning with eight weeks of age. Data obtained are presented below.

Sire	Dam	Test boars	Dam total	Sire total
A	1	4.8, 4.0, 3.8	12.6	33.7
	2	4.0, 3.2, 3.5	10.7	
	3	3.2, 3.7, 3.5	10.4	
B	4	3.7, 4.0, 4.7	12.4	37.4
	5	3.5, 4.2, 4.5	12.2	
	6	4.6, 4.0, 4.2	12.8	
C	7	3.4, 4.0, 4.0	11.4	34.4
	8	3.7, 4.3, 3.6	11.6	
	9	3.4, 4.1, 3.9	11.4	
D	10	4.8, 4.0, 3.8	12.6	36.5
	11	4.5, 4.4, 3.7	12.6	
	12	3.9, 3.6, 3.8	11.3	
E	13	4.0, 3.7, 3.8	11.5	37.9
	14	4.4, 4.6, 4.5	13.5	
	15	4.3, 4.0, 4.6	12.9	
F	16	4.8, 4.0, 3.8	12.6	36.3
	17	3.7, 3.9, 4.7	12.3	
	18	3.4, 4.0, 4.0	11.4	

$N = 54, S = 6, D = 18, E_x = 2162, EX^2 = 87512$

Compute the rest analysis of variance and estimated the component and h^2 . Remember the degree of freedom is $s-1$, Dam-sire, N-Dam.

SS_{dam} is calculated as $EX_{dam}^2 - SS_{sire(uncorrected)}$ not correction factor. $SS_{error} = SS_{total} - SS_{sire} - SS_{dam}$

$$S.E h^2 = 4 \times \sqrt{\frac{2}{(dk)^2} \left(\frac{MSS^2}{s-1} + \frac{MSD^2}{d-s} \right)}$$

$$\sigma_i^2$$

REPEATABILITY

When more than one measurement of a character can be made on each individual, the phenotypic variance can be partitioned into variance within individuals and variance between individuals. The partitioning leads to a ratio of variance components called repeatability which has three main uses. 1 it shows how much is to be gained by the repetition of measurements, 2. It set an upper limit to the ratios VG/VP and VA/VP and 3. it predicts future performance from past records. Repeatability therefore, expresses the proportion of the variance of a single measurement that is environmental. There are two assumptions implicit in the idea of repeatability, 1 is that the variances of the different measurements are equal, and have their components in the same proportions. 2. The second is that the different measurements reflect what the same character is genetically. The partitioning of the variance corresponding to the repeatability is not a part of genetic theory, because it is the environmental, not the genetic variance that is partitioned. It does however, have some practical implications for genetical analysis and breeding programme.

An analysis of variance is then made by which the phenotypic variance is divided into observational components attributable to differences between the individuals (the between individual component, (σ_b^2) , and within individual repeated values (within Individual components, σ_w^2).

Source	df	Means square	Composition of mean squares
Between Ind.	$b - 1$	MSB	$\sigma_w^2 + k \sigma_b^2$
Between dams	$N-(b-1)$	MSW	σ_w^2

$$\sigma_w^2 = MSW$$

$$\sigma_b^2 = \frac{MSB - MSW}{K}$$

K

$$R = \frac{\sigma_w^2}{\sigma_w^2 + \sigma_b^2}$$

Example: (Birth Weight yield in sheep)

Weight of birth of three consecutive offspring of seven sheep were obtained after birth for each animal. The data is as shown below. Estimated the repeatability of birth weight among these sheep population.

No of births	SHEEP						
	1	2	3	4	5	6	7
1	4.18	3.3	3.85	4.37	3.42	3.26	3.62
2	3.89	3.75	3.59	3.89	3.86	3.84	3.34
3	3.61	3.31	3.39	3.63	4.02	3.48	3.79
$\sum X$	11.68	10.36	10.83	11.89	11.30	10.58	10.75

GENETIC BY ENVIRONMENTAL INTERACTION

A genetic by environmental interaction exists when the ranking order of individuals or breeds changes in different environments. If on pasture, the ranking of seven bulls was 1, 2, 4, 5, 6, 3 and 7 but on concentrate diet the ranking order was 7, 3, 6, 5, 2, 4 and 1. There would have been an almost complete reversal and it would be unwise to select other than in the environment in which the bulls were to be used. In other words, if the results of comparisons vary depending on the environment in which they are conducted, we say there is interaction. The variation in results may involve just a change in relative performance or a change in ranking. The problem with GXE is that in many cases, it is difficult to predict in advance, whether or not such interaction is likely to be important. Because there are so many environment and genotypes, it is impossible to say that the genotype-environment interaction will not occur in a species. Experimental evidence suggests that dairy and beef cattle have few important genotypes by environmental interactions whereas they are more important in pigs and sheep. If GXE interactions are important, then, it is usually better to select in the environment where stock will be used. If stocks are used in widely differing environments, climates and managements regimes. There is a great responsibility upon breeders to be aware of the possibilities of these interactions. When interaction between genotypes by environment is present, the phenotypic value of an individual is not simply $P = G + E$, but includes also an interaction component $P = G + E + I_{GE}$. The interaction component give rises to an additional source of variation becomes.

$$V_P = V_A + V_E + 2COV_{GE} + V_{GE}$$

Genotype X environment interaction becomes very important, if individuals of a particular population are to be reared under different conditions. For example, a breed of livestock may be used by different farmers who treat it differently and varieties of plant are grown in different season at different places and under different conditions. The situation is different.

BREEDING SYSTEMS

Livestock breeders have two basic tools to work with. The basic tools are selection and mating systems. In a large animal population e.g. herd or a flock, the breeder often plan of how to get the best animal for genetic improvement. This is called selection. ***Selection is choosing the individuals that will have an opportunity to reproduce and consequently pass their genes on to future generations.*** Following selection, breeder must decide upon the manner in which the selected individuals are to be mated. The different pairing methods of the selected animals for improved performance is called breeding systems or mating systems.

At times, breeders can decide whether to mate animals of the same breed or mating different breeds; and if choosing the first policy, he can decide whether to mate related or unrelated individuals.

Whether choosing mating the same breed or different breeds, there are however several possibilities.

Breed

Breed refers to a group of animals within a species which have certain characteristics in common which render individual of that breed recognizable as such. Most of these characteristics are physical ones connected with coat colours. Many breeds have arisen because physical isolation has left some population separated and hence selection has caused distinctions to appear. Other breeds have evolved by crossing among older established breeds until a new type has emerged.

COMMON BREEDING SYSTEM

The two most common breeding system used for all species of livestock are:

- (i) Purebreeding and
- (ii) Crossbreeding

Breeding activities that involve mating the same breed is called purebreeding, while systematic or unsystematic mating of different breeds is called crossbreeding. Under each breeding system, there are different mating systems that are possible.

Purebreeding involves mating of relatives or mating of unrelated stock. Mating of relatives include (i) **inbreeding** and **line breeding** and these two forms of purebreeding is also known as **genetic assortative mating**.

Mating of unrelated stock includes:

- i. Outbreeding and
- ii. Outcrossing and

these two methods are also known as **genetic disassortative mating**

Mating of unrelated stock also include mating of likes with likes or mating the best to the best, or mating the worst to worst, but usually the worst are discarded from the breeding programme. This type of mating is also called **phenotypic assortative mating**.

Also included in the mating of unrelated stock is the mating of unlike to unlike and this is often called phenotypic disassortative mating or **compensatory mating**.

When the best animals have been selected from the herd or from the flock, there are many ways in which breeding individuals may be paired for mating.

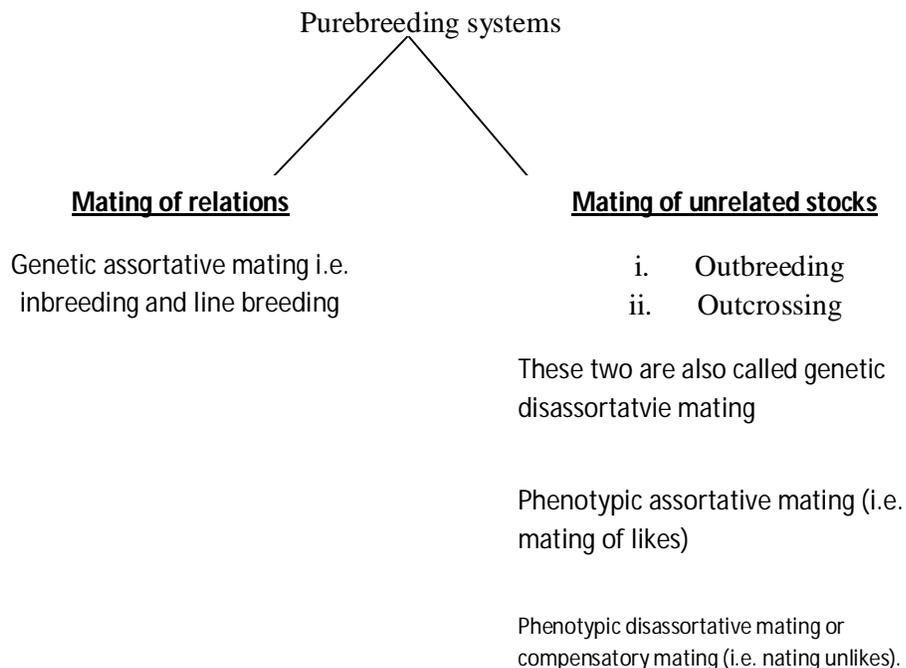
- They may be paired purely at random
- They may be paired by genetic relationship so as to be either genetically alike or genetically unlike.
- They may be paired on the basis of the phenotypic resemblance or distinctiveness.

Based on these, there are five basic types of mating systems and they are:

- a. Random mating
- b. Genetic assortative mating (i.e inbreeding and line breeding)
- c. Genetic disassortative mating (i.e. outbreeding and outcrossing)
- d. Phenotypic assortative mating (i.e. mating of likes)
- e. Phenotypic disassortative mating (i.e. mating of unlike to unlike). This is also called compensatory mating.

Any of these five kinds of mating systems can be practiced singly or in alternation with any of the others. They are almost always used in conjunction with various kinds of selection.

It must be noted that (b to e) above are purebreeding activities i.e.



In summary, the following mating systems are purebreeding systems.

- Inbreeding
 - Line breeding
- } **Genetic assortative mating or mating relatives**
- Mating like → phenotypic assortative mating
 - Mating unlikes → phenotypic disassortative mating

RANDOM MATING

This is the simplest of all the mating systems. Mating is random when mates are no more and no less alike, either as individuals or in pedigree, than if they had been mated by drawing lots from within the group selected to be parents i.e. any one individual of one sex is equally likely to mate with individual of the opposite sex. Random mating assumes that all individuals are equally viable and there is no differential fertility i.e. all individual contribute an equally number of offspring to the next generation and such random mating is termed **Panmixia**.

GENETIC ASSORTATIVE MATING

In this mating system, pure breeders use individuals of the same breed. They often used closely related (inbred or linebred animals for this purpose. This system of mating is usually called **Inbreeding**.

Inbreeding is the mating of individuals that are more closely related in descent than randomly chosen mates. The chances are that the closer the relationship, the more the individuals will possess characteristics in common.

If each has the same parent, each will carry on average half the genes of each parent. In farm animals, the closest relationship that can be procured will be brother X sister, sire X daughter or dam X son. Inbreeding increase homozygosity as the number of genes in common is increased in every generation.

MEASURE OF INBREEDING

The quantitative measure of the degree inbreeding is known as coefficient of inbreeding, often designated as F. This measures the amount by which heterozygosity is reduced under various types of genetic assortment. **The coefficient of inbreeding can be defined as the proportionate reduction in the heterozygosity relative to the original population.** Inbreeding coefficient can also be defined as the probability that the two genes at a locus are identical by descent, in the sense that both genes are the replicates of the same gene in the previous generation. It must be noted that F has value of zero in random mating population and increases toward one as the heterozygosity reduces to zero.

The coefficient of inbreeding is an attempt to measure the degree of homozygosity in an individual. The formula often used for the computation of inbreeding coefficient (F) is designated as

$$F_x = \frac{1}{2}(n_1 + n_2 + 1)(1 + F_A)$$

Where

F_x = inbreeding coefficient

n_1 = Number of intervening generations from sire to the common ancestor

n_2 = number of intervening generations from common ancestors to the dam

F_A = inbreeding coefficient of the common ancestor. In using this formula well, at times, arrows diagram may have to be constructed from pedigree.

EFFECTS OF INBREEDING

1. Inbreeding makes more pairs of genes homozygous regardless of the kind of gene action involved. Inbreeding do not change the gene frequency in the population, but causes an increase in the frequencies of homozygous genotypes and a decrease of heterozygous genotypes which ultimately will lead to the fixation of alleles.
2. Inbreeding uncovers the recessive genes which previously were concealed in the heterozygous condition. Though inbreeding do not create recessive genes, but most recessive genes have less desirable effects than their dominant alleles, inbred individuals usually show less average merit than non-inbred individuals.
3. Inbreeding leads to a decline in the mean phenotypic value of fitness traits. If inbreeding is undertaken, traits like fertility could decline, embryonic mortality may increase, progeny survival or viability could decline, growth rate may be lessened, milk yield may decline, but carcass traits might be unaffected.

REASON FOR PRACTISING INBREEDING

Though the general effects of continued inbreeding or genetic assortative mating are undesirable, but inbreeding has an important place in both animal and plant breeding. The gains of it are:

1. It tends to form distinct families so that inter family selection may be possible in a more effective way.
2. It is powerful in forming inbred line
3. It is useful in detecting the carriers of recessive genes.
4. Inbreeding increases prepotency (i.e. the ability of an individual to stamp its own characteristics on the offspring so that they resemble that parent and each other more closely than usual).
5. It is useful in the production of genetically uniform material for use in research in physiological and nutritional fields

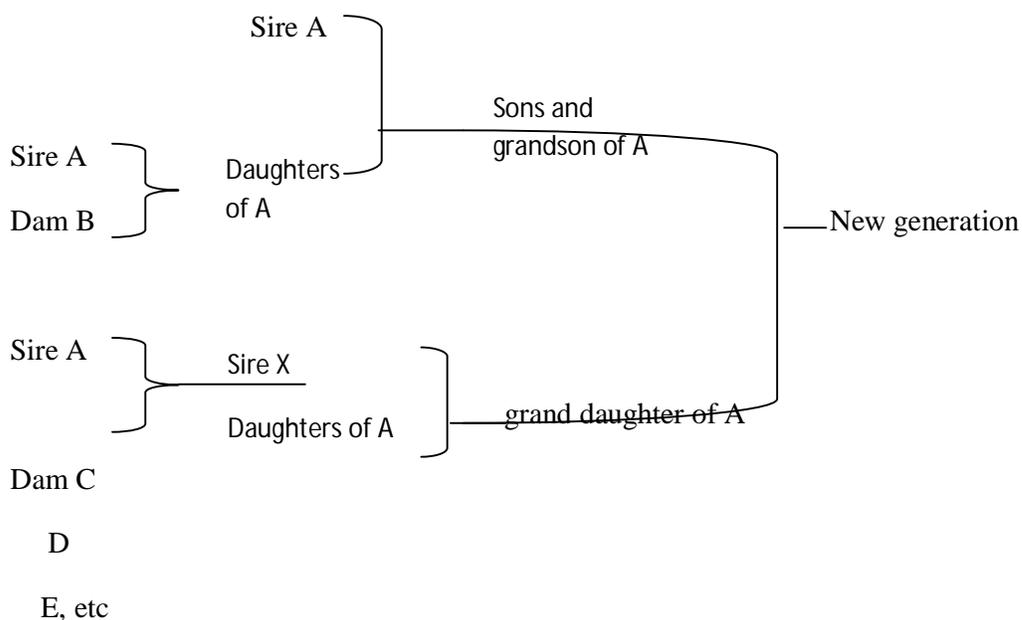
6. Inbreeding is of value in determine the type(s) of gene action that affect the various economic traits, if inbreeding effects are very small or non-existent, the trait is affected mostly by additive gene action, if inbreeding effects are very great, the trait is affected by non-additive gene action

LINE BREEDING

This is a milder form of inbreeding in which the relationship of an individual is kept close to some admired or outstanding ancestor in the pedigree. The admired ancestor is usually a male rather than female because a male generally produces many more offsprings than a female.

In reality, inbreeding and line breeding are the same thing; they only differ in degree. If inbreeding is dangerous, line breeding will be less so. If inbreeding succeeds, then line breeding will succeed more slowly.

A schematic line breeding is shown below



Other forms of purebreeding systems involve mating unrelated stocks.

These include:

- Genetic disassortative (outbreeding and outcrossing)
- Phenotypic assortative mating (i.e. mating likes) and
- Phenotypic disassortative (i.e. mating unlikes) or what is popularly known as compensatory mating.

GENETIC DISASSORTATIVE MATING

This means that mated pairs are less closely related than they would be under random mating. Only two of these mating systems have practical significance in animal breeding activities. These are the outbreeding and outcrossing. Outbreeding is the mating of unrelated individual within the same breed and outcrossing is the system of outbreeding carried out by breeder to offset the adverse effects that may accompany inbreeding. Outcrossing is the system of mating used by purebred breeders to obtain the same results within a breed as the commercial breeder does by crossing breed.

The general effects of outbreeding are exactly the opposite of those of inbreeding. While inbreeding increase homozygosity, outbreeding tends to increase heterozygosity for all of the pairs of genes when the parents possess different alleles. The practical usefulness of outbreeding rest with the fact the favourable effects of gene are generally dominant over the unfavourable ones.

PHENOTYPIC ASSORTATIVE MATING (i.e. MATING LIKES)

Mating of like to like is called phenotypic assortative mating. It is undertaken where breeders seek to mate animals with the same virtues. It is often called mating the best to the best and also involves mating worst to worst, but usually the worst are discarded from breeding programme in some selection that needs to be carried out. This system does not alter the gene frequency. In this system, individual mated are more similar for some phenotypic traits than if they were chosen at random from the population.

EFFECT OF PHENOTYPIC ASSORTATIVE MATING

1. Just like inbreeding causes increase in homozygosity, phenotypic assortative mating causes increase in homozygosity but to lesser extent or degree.
 2. The resemblance between close relative is very much increased.
- The advantage of phenotypic assortative mating is that it helps to reduce or eliminate the population of worst animal from the herd/flock.

PHENOTYPIC DISASSORTATIVE MATING (i.e. MATING UNLIKES OR COMPENSATORY MATING)

This is the mating of individuals that are more dissimilar for some phenotypic traits than they would be under random mating. It is popularly called mating unlike to unlike or compensatory mating. It is used at times to correct failings or compensate for defects in an excelling where the first fails. This policy or mating of unlikes, increase the uniformity in the population. Just like mating of like, mating of unlikes has limited influence in altering gene frequency. The effect of this mating is exactly opposite to those of phenotypic assortative mating.

BREEDING SYSTEM THAT INVOLVE MATING DIFFERENT BREEDS

(CROSSBREEDING)

Apart from purebreeding, the other breeding system is crossbreeding and this involves systematic or unsystematic combination of two or more breeds. The possible mating systems that involves mating of different breeds include (1) Crossbreeding (2) Grading up and (3) Topcrossing (4) Backcrossing (5) Crisscrossing (6) Rotational crossing (7) Lauprecht system.

CROSSBREEDING

Crossbreeding is the mating of individuals of two or more different breeds. Also, when unrelated livestock are mated, the system is known as crossbreeding. The basis of crossbreeding is the exploitation of hybrid vigour or heterosis. The progeny of crossbred livestock are heterozygous for those traits that differ in their parents and the greater the difference between parental traits, the greater the degree of heterozygosity in the offspring. Usually, first cross progeny are superior to the inferior parent in productive traits and often to both parents. This level of superiority is called **heterosis or hybrid vigor**. Hybrid vigour disappears very rapidly when hybrid are mated *inter se*, therefore new parental stock are continuously required if the livestock owner wishes to exploit hybrid vigour to the utmost level.

The genetic effects of outbreeding and crossbreeding are both similar. The general effects of outbreeding and crossbreeding are exactly the opposite of those of inbreeding. Whereas inbreeding tends to make more pairs of genes homozygous, outbreeding and crossbreeding tend to increase heterozygosity for all pairs of genes when the parents possess different alleles. Crossbreeding is therefore a form of genetic disassortative mating.

USEFULNESS OF CROSSBREEDING PROGRAMME

- Indigenous low-producing livestock can be upgraded by continuously backcrossing then to more highly productive introduced exotic stock.
- Through crossbreeding, crossbreds can easily be generated.
- Attempt may be made to create new and more productive breeds by crossbreeding indigenous and exotic livestock, mating *inter se* at either the first generation or after one or more backcross generations and then selecting the type of animal required.
- Advantage may be taken of hybrid vigour by some form of systematic cross breeding between two or more breeds of indigenous livestock or between an indigenous and an introduced breed.
- Through crossbreeding, increase in productivity may be achieved with little increase in economic input.
- A slowly increasing impact of inbreeding depression in established breeds may be countered by introduction of a crossbreeding programme.

GRADING UP (UP GRADING) AND TOPCROSSING

Grading up and top crossing are two techniques that are very similar. Topcrossing refers to a breeding system in which the breeders return to the original line to gain new genetic material (i.e. topcrossing is the mating of a male of a specified family to females of another family of the same breed); while upgrading is the method of choice when a livestock owner wishes to change radically the characteristics of his animal. It is the gradual changing of a breed by continued crossing with another. This method is common in the world over to upgrade one breed and convert it to another.

In upgrading, males of exotic type say animal (E) are mated generation after generation to indigenous and crossbred females say animal (I). As this continues, at F₄ generation the livestock are almost entirely of the exotic type (i.e after four crosses, the animal would be 93.8% pure), but the better sires used in such programme, the better the end product. In this case, the major effect of heterosis is in the F₁ generation (i.e. the original crossbred). Crossing F₁ with F₁ to give F₂, result in reduced heterosis. Accordingly, heterotic effects in grading up are eventually lost since the net effect is to change from one purebred to another.

A schematic illustration of upgrading system involving indigenous stock (I) with exotic stock (E) is shown below:

Generation	Mating types
	(100%I) x (100%E)
F1	(50%I: 50%E) x (100%E)
F2	(25%I: 75%E) x (100%E)
F3	(12½I: 87½E) x (100%E)
F4	(6¼:93¾E) x (100%E)

Even from F₄, the crossing can continued in a similar manner.

BACKCROSSING

Backcrossing is the mating of crossbred animals successively back to one or other of the same pure parent breeds which were initially crossed to produce it. The result slaughter generation is 75% of one breed and 25% of the other. The purpose of backcrossing is to recover the genotype of the recurrent parent, except for the addition of a gene or genes for the superior character from the non-recurrent parent. Backcrossing is just a scheme intended to take advantage of using a crossbred dam.

CRISSCROSSING (TWO BREED ROTATION SYSTEM)

Crisscrossing is also known as **two-breed rotation system** or the **up and down grading**. Crisscrossing is an extension of the backcrossing system. It involves the use of sire of two breeds in rotation on crossbred females. With this system of breeding, an attempt is made to utilize heterosis i.e exploitation of hybrid vigour in the females without the full decline in the average individual merit which usually occurs when crossbreds are mated together.

Crisscrossing is a breeding system that involves the rotational use of sires of one breed during one generation, followed by the use of sires of a second breed during the next generation and so on. In crisscrossing, two breeds say A and B are crossed. The crossbred is then mated back to B to give 75% B 25%A. This crossbred is then mated to A to give 62½% and 37½B. Thereafter, breeds A and B are used in alternate generations. A schematic representation of crisscrossing is shown below:

Generation	Mating types
	(100% A) x (100%B)
F1	(50%A: 50%B) x (100%B)
F2	(25%A: 75%B) x (100%A)
F3	(62½%A: 37½%B) x (100%B)
F4	(31¼%: 68¾%B) x (100%A) and
so on.	

Advantages of crisscrossing or rotational crossbreeding system

1. Crisscrossing is more productive because it exploits hybrid vigour to the maximum
2. Crisscrossing or rotational crossbreeding programme inhibits gene recombination
3. It facilitates the use of sires of two breeds on crossbred females

Disadvantages

1. Breeder must have access to sires or semen from two or more breeds and this complicate management of breeds
2. It is very difficult to operate rotational crossbreeding under smallholder conditions. It is only confined to large holdings that is often difficult to be practiced by many farmers.

COMPLEX ROTATIONAL CROSSING (i.e. THOSE INVOLVING USE OF MORE THAN TWO SIRE BREEDS).

In this system, series of breeds (three, four or more) are used in succession. In principle, by using several breeds there ought to be greater heterosis than by using a two breed backcrossing or crisscrossing policy. Complex rotational crossing involving three or more breeds has proved somewhat superior to backcrossing or crisscrossing methods that make uses of only two breeds.

However, much will depend upon the breeds available in any species and their compatible. Though, the advantage of this system is that there is increased hybrid vigour, but it becomes impracticable when farmers do not have access to several breeds. Management of several breeds is also more complicated that two breed rotational system. A complex rotational system involving more than two breeds is shown below:

Example: Rotation crossing using five breeds

Female		Male
Hereford (H)	x	Limousin (L)
HL	x	Simmental (S)
HLS	x	Charolais (C)
HLSC	x	Brown Swiss (B)
HLSCB	x	Hereford (H)

LAUPRECHT SYSTEM

Though, Lauprecht is an unusual programme, but it has been in practice in few farms since developed by German scientist, Lauprecht in 1961.

Lauprecht programme involve using three breeds (A, B, C). A is crossed with B and the resultant crossbred mated to C. thereafter, the policy is different to other programme because

only crossbred males are used and in each case the female generation is mated to males from previous crossbred generation. A representation of this crossing is shown below:

A x B

AB x C

ABC x AB

AABBC x ABC

AAABBBC x AABBC and so on.

Limitation of this programme

- More complex
- It is time consuming
- The resultant effectively becomes a new breed rather than a distinct crossbred

DEVELOPMENT OR CREATING NEW BREEDS

The development of a new breed may be accomplished by the crossbreeding of two breeds of a specific type of livestock, followed by backcrossing one way or the other to attain the planned cross of the parent breeds. At this stage, the crossbreds must be mated *inter se* followed by intense selection among their progeny for the type of animal required. A number of new beef and dairy cattle breeds have been evolved using this technique. Some new beef cattle breeds developed include:

Name of beef cattle	Composition	Origin
Brangus	5/8 Angus/3/8 Brahman	USA
Charbray	5/8 Charolais/3/8 Brahman	USA
Santa Gertrudis	5/8 Shorthorn/3/8 Brahman	Texas
Luig	5/8 Shorthorn/3/8 Highlands	Scotland

Note: Brahman = Zebu derived strain

Some new dairy breeds developed include the following:

Name of some new dairy breeds	Composition	Origin
Jamaica Hope dairy	70% Jersey / 20% Sahiwal / 10% Holstein	Jamaica
Australian Milking Zebu (AMZ)	5/8 Jersey / 3/8 Zebu	Australia
Siboney de Cuba	5/8 Holstein / 3/8 Zebu	Cuba

Most often, there has been deliberate attempt to use about 5/8 *Bos taurus* (humpless) and 3/8 *Bos indicus* (humped cattle) in the development of new breed, but it must be noted that there is nothing magical about this particular combination. It must be noted that the new breeds development are crossbreeds. For Siboney de Cuba for instance, it was developed using

Zebu cow x Holstein bull
(100%) (100%)

F1 ← (50% Holstein / 50%Zebu) x 100% Zebu bull

F2 ← ¾ zebu ¼ Holstein x 100% Holstein bull

F3 ← 3/8 zebu 5/8 Holstein (or Siboney de Cuba dairy cattle)

Though, development of new breed of animal for specific environmental conditions appeared highly attractive, but it takes too long a time to develop some new breeds and by the time a new breed is eventually developed, conditions might have been changed by improved plane of nutrition and management techniques.

Selection

Selection is an important tool for changing gene frequencies to better fit individuals for a particular purpose. It may be defined as a process in which certain individuals in a population are preferred to others for the production of the next generation.

Selection is of two general kinds, natural, or that due to natural forces, and artificial, or that due to the efforts of man.

Natural Selection

In nature, the main force responsible for selection is the survival of the fittest in a particular environment. Natural selection may be illustrated by considering the ecology of the relationship between wolves and the Dall or mountain sheep. Apparently, the wolves chase many sheep before they find one they can catch. Most of those killed by the wolves are the weaker animals, and included those that are either very young or very old. Thus, there is a tendency for nature to select against the weaker ones, and only the stronger survived to reproduce the species.

Some of the most interesting cases of natural selection are those involving man himself. All races of man that now exist belong to the same species, because they are inter-fertile. All races of man now in existence had a common origin, and at one time probably all men had the same kind of skin pigmentation. As the number of generations of man increased, mutations occurred in the genes affecting pigmentation of the skin, causing genetic variations in this trait over a range from light to dark or black. Man began to migrate into the various parts of the world and lived under a wide variety of climatic conditions of temperature and sunshine. In Africa, it was supposed, the dark-skinned individuals survived in larger numbers and reproduced their kind, because they were better able to cope with environmental conditions in that particular region than were individuals with a lighter skin. Likewise, in the northern regions of Europe men with white skins survived in a greater proportion, because they were better adapted to that environment of less intense sunlight and lower temperatures.

Recently, evidence has been obtained that there may be a differential selection for survival among humans for the A, B, and O blood groups. It has been found that members of blood group A have more gastric carcinoma (cancer) than other types and that members of type a have more peptic ulcers. This would suggest that natural selection is going on at the present time among these different blood groups, and the frequency of the A and O genes might be gradually decreasing unless, of course, there are other factors that have opposite effects and have brought the gene frequencies into equilibrium.

Natural selection is a very complicated process, and many factors determine the proportion of individuals that will reproduce. Among these factors are differences in mortality of the individuals in the population, especially early in life; differences in the duration of the period of sexual activity; the degree of sexual activity itself; and differences in degrees of fertility of individuals in the population.

Artificial Selection

Artificial selection is selection practiced by man. It may be defined as the efforts of man to increase the frequency of desirable genes, or combinations of genes, in his herd or flock by locating and saving for breeding purposes, those individuals with superior performance or which have the ability to produce superior performing offspring when mated with individuals from other lines or breeds. Even when artificial selection is practiced, natural selection also seems to have a part. Artificial selection in farm animals are of two kinds, one known as *automatic* and the other as *deliberate selection*. Litter size in swine may be used as an illustration of the meaning of these two terms. Here, automatic selection would result from differences in litter size even if parents were chosen entirely at random from all individuals available at sexual maturity. Under these conditions, there would be twice as much chance of saving offspring for breeding purposes from a litter of eight than from a litter of four. Automatic selection here differs from natural selection only to the extent that the size of the litter in which an individual is reared influences the natural selective advantage of the individual for other traits. Deliberate selection, in this example, is the term applied to selection in swine for litter size above and beyond that which was automatic. The opportunity for deliberate selection among pigs is utilized more fully for growth rate. Differences between breeds and types of farm animals within a species is a proof that artificial selection has been effective in many instances.

Genetic Effects of selection

Selection does not create new genes. Selection is practiced to increase the frequency of desirable genes in a population and to decrease the frequency of undesirable genes. This may be illustrated by the following example, where A is the desirable gene and a the undesirable gene:

P	AA	X	aa
F_1			All Aa
			(Freq. of A is
F_2	Aa	X	Aa

Progeny: 1 AA

2 Aa

1 aa

Freq. of gene A in F_2 is still 0.50.

Let us assume that we cull all aa individuals in the F_2 . If this were done, the remaining genes would be four A and two a . Thus, the frequency of the A gene would be increased to 0.67 and that of the a gene would be decreased to 0.33. The increased frequency of the A gene when the aa individuals were culled would also increase the proportion of AA individuals in the population. If the frequency of the A gene were 0.50 (if it is assumed that requirements of the Hardy-Weinberg Law were met), the proportion of A individuals would be 0.50 multiplied by 0.50 or 0.25. However, if the frequency of the A gene were increased to 0.67, the proportion of AA individual would be 0.67 multiplied by 0.67 or 0.449. If selection is effective, the genetic effects of selection are to increase the frequency of the gene selected for and to decrease the frequency of the gene selected against. If the frequency of the desirable gene is increased, the proportion of individuals homozygous for the desirable gene also is increased.

SYSTEMS OF SELECTION FOR DIFFERENT KINDS OF GENE ACTION

Different kinds of gene actions affect economic traits in farm animal. In certain instances (e.g. coat color and horns) only one pair of genes, or relatively few genes, exert major effect traits of great economic importance. Sometimes single pair of genes may also have a major phenotypic effect on certain quantitative traits. An example is the gene for snorter dwarfism in beef cattle where a pair of recessive genes (dd) may produce a dwarf, hiding or masking the phenotypic expression of many additive genes for fast growth and potential large mature size. In quantitative traits determined by many pairs of genes, some of these genes may express themselves in an additive manner, whereas others may express themselves in a non additive way. Because both qualitative and quantitative traits may be greatly affected by many different types of gene action, it is important here to outline what methods may be used in selecting for or against them.

Selection For a dominant gene

In practice, we are very likely to be selecting for a dominant gene, because traits determined by such genes are usually desirable. Those individual possessing a dominant gene will show

it, but the problem here is one of distinguishing between the homozygous dominant and heterozygous dominant individuals. The heterozygous individuals must be identified by a breeding test or a knowledge of the parental phenotype in some cases before they can be eliminated. Selection for a dominant gene involves the same principle as selection against a recessive gene.

Selection for against dominant gene

Selection against a dominant gene is relatively easy, providing the penetrance of the gene is 100 percent and it does not vary in its expression. Since each animal possessing a dominant trait should show this in its phenotype, eliminating the gene merely means that all animals showing the trait should be discarded. Whether or not this can be done at once, of course, depends upon the number of animals possessing the trait and whether one can afford to discard all of them at one time.

If the penetrance of the gene is low and the genes are variable in their expression, selection against a dominant gene would be much less effective. Selection for such a trait could not be based upon the individual's phenotype alone, but attention to the phenotype of the ancestors, progeny, and collateral relatives would also be necessary if selection were to be successful.

Selection for a recessive gene

Selection for a recessive gene is relatively simple, if penetrance is complete, if the genes do not vary too much in their expression, and if the frequency of the recessive gene is relatively high. Selection under such conditions is merely a matter of keeping those individuals which show the recessive trait. A good example of such selection would be for the horned gene in cattle. To produce all horned cattle, one merely has to obtain horned breeding stock and mate them together. The only time polled individuals would be produced from such a mating is when a mutation from the horned to the polled gene occurs. This is so infrequent that it is seldom observed in an average size herd.

Selection against a recessive gene

Selection against a recessive gene is the same as selection for a dominant gene. In both instances the homozygous recessive individuals can be identified and discarded. Even when this is done, the recessive gene still remains in the herd, or population, being possessed by heterozygous dominant individuals. To eliminate the recessive gene entirely, the homozygous recessive and heterozygous dominant individuals both must be discarded, leaving only the homozygous dominant individuals.

Discarding or culling all homozygous recessive individuals reduces the frequency of the recessive gene but does not eliminate it. However, if the heterozygous dominant individuals in the population are preferred in selection, the frequency of the recessive gene may increase in spite of the fact that all homozygous individuals are eliminated.

Selection for genes with Epistatic effects

Epistasis is the interaction between genes which are not alleles. These interactions may be of several different kinds. They may be either complementary or inhibitory, but we do not know for certain in what manner the genes may act, as far as their influence on the important economic traits in farm animals is concerned. We do have evidence, however, that epistasis may be of considerable importance in determining the performance of farm animals.

Selection among families, lines, or breeds to find those that would give superior progeny would be the desired way of selecting for epistatic gene action. First, several different

unrelated lines should be formed by inbreeding, which serves to make them homozygous for more of the pairs of genes they possess. Once these inbred lines are formed, they should be tested in crosses to find those that "nick," or combine, the best as indicated by the production of superior F_1 progeny. Once two or more lines are found that cross well, they can be retained as pure inbred lines and crossed again and again for the production of offspring for commercial purposes. This is the procedure followed in the production of hybrid seed corn. The formation of many inbred lines, testing these in crosses to find those that combine the best, then combining these lines by crossing and inbreeding and selecting within the crosses should be helpful in developing superior inbred lines if epistasis is important. This procedure is probably too time consuming and expensive to be of much practical value in farm animals.

SELECTION FOR A SINGLE QUANTITATIVE TRAIT

Quantitative traits are those affected by several pairs of genes, many of which have small individual phenotypic effects. The phenotype of such traits may be affected by additive or non-additive gene action, or both. The phenotypic expression of such traits is also affected by environment. The amount of genetic progress (ΔG) made in one generation of selection for a quantitative trait depends upon the heritability (h^2) of the trait multiplied by the selection differential (Sd) for that trait. Thus the genetic progress expected in one generation of selection would be

$$\Delta G = h^2 \times Sd$$

The selection differential (Sd) refers to the superiority, or inferiority, of those selected for parents (P_s) as compared to the average of the population (\bar{P}) from which the breeding animals were selected. The selection differential is also sometimes referred to as the *reach* and may be denoted by the following formula:

$$Sd = (P_s - \bar{P})$$

For example, if the average daily gain in a group of full fed calves is 2.00g and in those kept for breeding is 2.50g, the selection differential would be 0.5g per day. If all animals were kept for breeding the selection differential would be zero and the expected genetic progress would be zero.

The selection differential may also be expressed in terms of standard deviation units, providing the frequency distribution curve for that trait is a normal bell-shaped curve. The formula would be

$$Sd = i\sigma_p$$

where i is the intensity of selection in standard deviation units and σ_p is the phenotypic standard deviation of the trait in the population from which the breeding individuals are selected. If the proportion of animals kept for breeding is known, the selection intensity i may be calculated from the formula $i = z/w$, where z represents the height of the curve, where the group of animals selected for breeding are separated and where w represents the fraction of the population selected for breeding. This is sometimes referred to as selection differentials under *truncation*, which means that all individuals above a certain production level are kept for breeding. The value of z may be obtained from tables showing the ordinates and area of the normal frequency distribution curve.

Table Showing changes in the selection differential as units of the standard deviation when different proportions of the total population are saved

<i>Fraction of all animals kept for breeding</i>	<i>Selection differential* as units of the standard deviation or the selection intensity i</i>
0.90	0.20
0.80	0.35
0.70	0.50
0.60	0.64
0.50	0.80
0.40	0.97
0.30	1.16
0.20	1.40
0.15	1.55
0.10	1.76
0.05	2.05
0.01	2.64
0.001	3.37

***The selection differential Sd equals $P_g - \bar{P}$ equals i times the phenotypic standard deviation σ_p . This assumes that the data fit a normal frequency distribution curve and that all animals above a certain value are kept for breeding (truncated).**

As an example, let us assume that the selection intensity i is 0.20 and the phenotypic standard deviation σ_p for yearling weight in a group of cattle is 95 g. The selection differential Sd would be 95 multiplied by 0.20, or 19 g. On the other hand if only 5 percent of the individuals were saved for breeding, the selection differential would be 95 multiplied by 2.05, or 194.75 g. Selection pressure would be much more intense in the latter case.

A number of factors may affect the size of the selection differential Sd . The smaller the proportion of individuals in the total population kept for breeding, the larger the selection differential. Since fewer males than females are kept for breeding, the selection differential for males will almost always be larger than for females

Selection Progress per year

The amount of expected genetic gain made over a period of time (ΔG) through selection depends upon the size of the selection differential Sd , the degree of heritability of the trait h^2 , and the length of the generation interval I_g . The formula used for computing the expected genetic gain over a period of time is as follows:

$$\Delta G = \frac{Sd \times h^2}{I_g}$$

The generation interval may be defined as the average age of the parents when their offspring which will produce the next generation are born. Or, defined another way, the generation interval is the time interval between the same stage in the life cycle of two successive generations.

The length of the generation interval varies with different species of animals and with the breeding and management systems followed to produce a new generation of breeding animals. The generation interval in swine can be reduced to one year if pigs are selected from the first litters of gilts bred to boars of the same age. If sows as well as boars are progeny-tested before they are used to produce breeding or replacement offspring, the generation interval may be two years or even longer. In cattle, the generation interval conceivably would be as short as 2.5 to 3.0 years, but on the average it is considerably longer if any progeny-testing is done or if the performance records of cows determine whether or not their offspring are kept for breeding purposes. Lengthening the generation interval in order to progeny-test the parents eventually serves to lower the selection differential over a period of time.

Genetic Correlations among traits

When we speak of genetic correlations among traits, we are referring to whether or not the same gene responsible for qualitative inheritance or some of the same genes responsible for quantitative inheritance affect two or more economic traits. Genetic correlations among traits are estimated by special statistical procedures or by selecting for one trait over a period of time and noting whether or not there is a change (correlated response) in traits not selected for as genetic improvement is made in the trait for which selection is practiced. Single-trait selection experiments must be carefully designed accurately to observe whether or not two or more traits are genetically correlated.

Pleiotropy is probably the major cause of genetic correlations, although it is possible for linkage to have a similar transitory effect. Pleiotropy is the process whereby one gene may affect two or more traits. Linkage means that the genes are carried on the same chromosome. Some genes may be so closely linked together on the same chromosome that they seldom, if ever, separate by crossing-over during synapsis in meiosis. Closely linked genes would tend to stay together over several generations, and the association of the traits determined by them would persist. Genes farther apart on the same chromosome would separate more readily by crossing-over during synapsis in meiosis, and the relationship of the traits determined by such genes would break up, or become transitory. If pleiotropy is the cause of genetic correlations this would suggest that the traits correlated would be affected by at least some of the same physiological pathways.

The genetic correlation between two traits may be very low, which means that probably very few of the same genes affect the two traits. Type and performance in beef cattle is a good example of this in that selection for type seems to have little influence on performance, or *vice versa*. Obviously, selection on the basis of one will not make an improvement in the other, and we might say that the two traits are inherited independently. If true, this means that it should be possible to get both in our animals, but to do so we must select for both.

Two or more traits may also be correlated from the genetic standpoint in a positive manner. By this is meant that selection for the improvement of one will also result in the improvement in the other, even though direct selection for its improvement has not been practiced. An example of this is rate and efficiency of gain in swine.

It is also possible for two traits to be genetically correlated in a negative manner. This means that selection for the improvement of one, if successful results in a decline in the other to which it is genetically correlated. An example of such a correlation is butterfat percentage and milk yield in dairy cattle.

Selection of superior breeding stock

Any progress to be made through the application of breeding and selection methods will depend upon the ability to recognize and mate those animals possessing superior inheritance for a particular purpose. Superior inheritance is indicated by the phenotypic merit of the individual or upon its ability to combine well with others for the production of superior F1 offspring.

Selection On The Basis Of Individuality

Selection based on individuality means that an animal is kept or rejected for breeding purposes on the basis of its own phenotype for a particular trait, or traits. The progress made in selection depends upon how closely the genotype is correlated with the phenotype. Sometimes this correlation is high, but there are times when it is low. The phenotype of the individual varies throughout its life because of environmental effects or the interaction between its genotype and environment. The genotype of an individual, however, is fixed at the time of fertilization and does not vary as does the phenotype.

The phenotype of the individual (individuality) is often used to estimate its breeding value. Selection for qualitative traits such as colour and horns or lack of horns on the basis of the individual's phenotype is more effective in some instances than in others. The genotype of the homozygous recessive individual, where only one pair of genes is involved, may be determined from its phenotype. The genotype of the individual carrying a dominant gene cannot be determined from its phenotype because we cannot distinguish phenotypically, between the homozygous dominant and the heterozygous dominant individual. Thus, selection on the basis of individuality for qualitative traits may be useful but it is not always completely accurate. Information on the phenotypes of the close relatives as well as that of the individual makes these estimates of the genotype more accurate. The same is true for quantitative traits. Quantitative traits are those affected simultaneously by many pairs of genes and various elements of the environment so that there is no sharp distinction among phenotypes of the individuals within a group. Such traits may be affected mostly by additive gene action or mostly by nonadditive gene action, or both.

In selection for quantitative traits the breeder attempts to estimate the genotype of the individual from its phenotype. If such a trait were 100 percent heritable, the phenotype and genotype of the individual for that trait would be identical. However, no quantitative trait is 100 percent heritable, because environment always affects the phenotype to a certain extent. The phenotypic merit of the individual for important economic traits (quantitative) is determined by comparing the individual's phenotype with that of the average of all individuals within a group from which it is selected. To be effective, the comparison must be made under carefully controlled environmental conditions with other animals of nearly the same age and at the same time.

Selection On The Basis Of Pedigrees

A pedigree is a record of an individual's ancestors related to it through its parents. In the past, most of the information included in pedigrees has consisted only of the names and registration numbers of the ancestors, and little has been indicated as to their phenotypic and genotypic merit. More recently, data to indicate the phenotypic merit of ancestors are being included in pedigrees. These pedigrees are called *performance pedigrees*. A study of pedigrees, if full information is available on the phenotypes and genotypes of the ancestors, may be of importance in detecting carriers of a recessive gene. Such information has been used with success in combating dwarfism (a recessive trait) in beef cattle. Cattle were sold on the basis of whether or not they were "pedigree clean" or "pedigree dirty." The latter term refers to an

animal having some ancestors that produced dwarfs and who, therefore, were carriers of the dwarf gene. This would indicate that the animal whose pedigree was being studied could also be a carrier of this gene.

A disadvantage of the use of the pedigree in selection against a recessive gene is that there are often unintentional and unknown mistakes in pedigrees that may result in the condemnation of an entire family of breeding when actually it may be free of such a defect. On the other hand, the frequency of a recessive gene in a family may be low and records may be incomplete, so that an animal appears to have a "clean" pedigree. Then, later, it will be found that the gene is present, and this family, once thought to be free of the recessive gene, will be called a "dirty" family. A definite disadvantage of pedigree selection as used in dwarfism in beef cattle is that all animals with the same or similar pedigree are condemned. This occurs in spite of the fact that individuals in such a line are free of the recessive gene, as proved by progeny tests. Nevertheless, the individual still has a questionable pedigree and will be discriminated against by many breeders, either because they are not familiar with the mode of inheritance affecting such a trait or because they are afraid to trust progeny-test information.

The use of records of the performance of ancestors to increase the accuracy of determining the probable breeding value of an individual can help increase the accuracy of these predictions under certain conditions. To be of value for this purpose, the records of the ancestors must give some idea of their merit as compared to that of their contemporaries, and the heritability of the trait must be something less than 100 percent. Since the heritability of a trait is never so high, good records on the performance of ancestors make predictions of the individual's breeding value more accurate. How much attention should be paid to the performance records of an ancestor depends upon the following factors: (1) The degree of relationship between the ancestor and the individual. (2) The degree of heritability of the trait. (3) Environmental correlations* among animals used in the prediction. (4) How completely the merit of the ancestors used in the prediction is known.

Statistically, the *accuracy of selection* as used here is an estimate of how accurately the genotype of the individual for certain traits can be predicted from the phenotypic average of its relatives. The relatives of an individual possess more genes in common with each other than non-relatives. Superior relatives give an indication that the individual also possesses superior genes, and he or she should transmit such genes to his or her progeny.

Pedigrees do have the advantage that they are cheap to use, they may be used to select for traits not expressed early in life such as cancer eye and longevity, and they may be used to select for traits expressed only in one sex such as milk and egg production.

Selection On The Basis Of Progeny Tests

Selection on this basis means that the breeder makes a decision to keep or cull a sire or dam based on the average merit of their offspring as compared to the average merit of the progeny of contemporary sires and dams. Progeny tests may be used in selection for both qualitative and quantitative traits

Probably the most effective use of progeny tests in selection for qualitative traits is to determine if an individual of the dominant phenotype is homozygous or heterozygous. To produce a pure breeding line or herd for a dominant trait or to eliminate all individuals carrying a recessive gene in the line or herd, one must discard all homozygous recessive individuals as well as the heterozygous individuals that, although possessing the dominant phenotype, are carriers of the recessive gene. The recessive individuals are identified from their phenotypes, but the heterozygous and homozygous individuals have similar phenotypes. The genotypes of these two dominant phenotypes must be determined through progeny tests

unless it is known that one parent is recessive. One can never be absolutely certain that an individual is homozygous dominant after it is progeny.-tested, but the more dominant offspring the individual produces without producing any that are recessive when certain test matings are made, the higher the probability that the individual is homozygous dominant.

In litters bearing animals both sires and dams may be progeny-tested. In all species where a sire can be mated to his own daughters, this has the advantage of progeny testing him for all detrimental genes he might possess and not for just a specific gene. Other matings (those not between related animals) test only for a specific gene. Thoroughly progeny-tested males that prove to be free of detrimental recessive genes could be used on a wide-scale basis for artificial insemination or for establishing new inbred lines.

Mating a male to his own unselected half-sisters is a method of progeny- testing to prove him free from any recessive gene he might have received from the parent that makes him related to the females to which he is mated. If he is mated to 23 different half-sisters and no homozygous recessive offspring are produced, one would say he was free of any recessive gene he might have received from their common parent at the 95 percent level of probability. He is tested free of these recessive genes at the 99 percent level of probability if he is mated to 35 different unselected half-sisters and produces no homozygous recessive offspring. If the frequency of a recessive gene in a population is high, the random mating of a sire to females in that population gives some indication of whether or not he is carrying a recessive gene. If the frequency of a gene is low, the probability of proving a sire free of a recessive gene is very low: Under practical conditions, the frequency of most detrimental recessive genes is low.

Mating a sire to his full-sibs will also test him for any recessive gene he might have received from both parents, providing that enough different full sisters are available for such a test.

Progeny tests may be used to predict more accurately the PBV of a parent for a quantitative trait. The principle involved in the progeny test is that each progeny receives a sample one-half of its inheritance from each of Its parents, and this is a sample one-half of the parent's breeding value. By increasing the number of progeny tested for a certain parent and calculating the average of these progeny, it is possible to obtain an estimate of the repeated parent's breeding value (usually a sire) based on this relationship.

Progeny tests are conducted to compare the performance of the progeny of two or more parents. Usually sires rather than dams are progeny-tested, because sires generally produce more progeny in a given season or year. The more carefully the progeny tests are conducted, the more accurate will be the determination of the PBV of the parents being compared.

Several precautions should be taken to make progeny tests more accurate.

- (1) Dams mated to all sires on a given progeny test should be selected randomly.
- (2) Standardize rations and feeding practices. Feed animals the same ration and in the same manner.
- (3) Do not feed all progeny of a single sire in the same pen. Some pens may be more favorable, or less favorable, for performance, and this tends to increase environmental variations among the different sire groups.
- (4) Compare different parent groups raised in as nearly the same environment or location as possible.
- (5) Compare parent groups born during the same year or same season of the year when possible.
- (6) Include all healthy progeny of a particular parent in the test, if possible, whether they are inferior or superior.
- (7) The larger the number of progeny tested per parent, within limits, the more accurate the estimate of that parent's PBV.

The accuracy of selection (which is the correlation of the genotype of the parent with the average phenotype of its progeny) may be calculated as follows:

$$\frac{h}{2} \sqrt{\frac{n}{1 + (n-1)t}}$$

where h is the square root of the heritability for a trait, n is the number of progeny per parent used in the average, and t is approximately $\frac{1}{4}h^2$ or $h^2/4$ if the progeny group is composed of half-sibs and there is no environmental correlation between sibs.

Selection On The Basis Of Collateral Relatives

Collateral relatives are those not directly related to an individual as ancestors or progeny. Thus, they are the individual's brothers, sisters, cousins, uncles, aunts, etc. The more closely they are related to the individual in question, the more valuable is the information they can supply for selection purposes.

Information on collateral relatives, if complete, gives an idea of the kinds of genes and combinations of genes the individual is likely to possess. Information on collateral relatives is used in selecting dairy bulls, since milk production can be measured only in cows even though the bull possesses and transmits genes for milk production to his offspring. Records on collateral relatives can also be used in the selection of poultry for egg and meat production and for all-or-none traits such as mortality, disease resistance, number of vertebrae, or fertility.

Selection on the basis of sib tests means that an individual is kept for breeding or is rejected (culled) on the basis of the average phenotype of its brothers and sisters. These may be maternal half-sibs, paternal half-sibs, or full sibs. The principles involved in the use of sib tests to estimate the PBV of an individual are similar to those used in pedigree and progeny selection.

The accuracy of selection on the basis of the phenotypes of sibs depends upon the degree of heritability (h^2) of the trait, the closeness of the relationship (R) of the sibs and the individual being selected, the number of Sibs (n) used to determine the sib average, and the degree of correlation (t) between the phenotypes of the sibs. The accuracy of selection may be calculated from

$$Rh \sqrt{\frac{n}{1 + (n-1)t}}$$

In using this formula we are assuming that no inbreeding is involved, and if the tests are designed in such a way that the environmental correlations among the phenotypes of the sibs are zero, t equals Rh^2 .

SELECTION FOR SPECIFIC COMBINING ABILITY

Selection for specific combining ability means that selection is practiced to take advantage of hybrid vigor when non-additive gene action is important. Selection on the basis of individuality usually is not the most efficient method of selection for traits affected largely by non-additive gene action. Increased merit in such traits usually depends upon heterozygosity through crossbreeding, resulting in the expression of hybrid vigor. If dominance is important, however, selection on the basis of individuality will be effective in improving traits within a breed. It is less effective if epistasis and overdominance are important.

In quantitative inheritance where many genes may affect the same trait, it is not possible to determine from the phenotype which animals are homozygous in opposite ways for many

genes. Certain methods may be used, however, to identify those individuals that are homozygous in opposite ways. The method probably most often used in finding lines or breeds that "nick" best when crossed is the method used in the production of hybrid seed corn. The first step is to form several different inbred lines by close inbreeding. Inbreeding increases the homozygosity of all pairs of genes that the individuals in an inbred line possess. If inbreeding were 100 percent within an inbred line, all individuals within that line should be homozygous for all the gene pairs they possess, regardless of the phenotypic expression of those genes. The breeder, of course, has no sure way of knowing what pairs of genes are homozygous within an inbred line. In practice this is not necessary.

The next step after inbred lines are formed is to test them in crosses to determine which lines combine to produce the best linecross progeny. In general, the two inbred lines producing the most superior progeny when crossed are the ones that are homozygous in opposite ways for many pairs of genes, giving greater heterozygosity in the progeny. These inbred lines are kept pure to cross again and again in later years to produce progeny that may be the source of commercial animals most of which are sold and not kept for breeding purposes.

Reciprocal recurrent selection is a system of selection for increasing the combining ability of two or more lines or breeds that have already demonstrated from past crosses that they "nick" or combine well. The principles involved assume that individuals in the two lines are not completely homozygous in opposite ways for all pairs of genes but that one allele may be present at a high frequency in one line and at a low frequency in the other line. Crossing the lines and selecting the individuals to reproduce each pure line on the basis of the performance of their crossbred progeny theoretically should make the two lines more homozygous in opposite directions. Reciprocal recurrent selection is described in Chapter 8 as a method of selection between lines, families, or breeds to take advantage of overdominance. In farm animals, selection is usually practiced for more than one trait.

METHODS OF SELECTION FOR MORE THAN ONE TRAIT

From the practical standpoint, the net value of an animal is dependent upon several traits that may not be of equal economic value or that may be independent of each other. For this reason, it is usually necessary to select for more than one trait at a time. The desired traits will depend upon their economic value, to a great extent, but only those of real importance should be considered. If too many traits are selected for at one time, less progress will be made in the improvement of any particular one. Assuming that the traits are independent and their heritability is about the same, the progress in selection for anyone trait is only about $\frac{1}{\sqrt{n}}$ times as effective as it would be if selection were applied for that trait alone.

Several methods may be used for determining which animal should be saved and which should be rejected for breeding purposes.

Tandem Method

In this method, selection is practiced for only one trait at a time until satisfactory improvement has been made in this trait. Selection efforts for this trait are then relaxed, and efforts are directed toward the improvement of a second, then a third, and so on. This is the least efficient of all methods from the standpoint of the amount of genetic progress made for the time and effort expended by the breeder.

The efficiency of this method depends a great deal upon the genetic association between the traits selected for. If there is a desirable genetic association between the traits, so that

improvement in one by selection results in improvement in the other trait not selected for, the method could be quite efficient. If there is little or no genetic association between the traits, which means that they are inherited more or less independently, the efficiency would be less than if the traits were genetically associated in a desirable manner. Since a very long period of time would be involved in the selection practiced, the breeder might change his goals too often or become discouraged and not practice selection that was intensive and prolonged enough to improve any desirable trait effectively. A negative genetic association between two traits, in which selection for an increase in desirability in one trait results in a decrease in the desirability of another, would actually nullify or neutralize the progress made in selection for anyone trait. Therefore, the efficiency of such a method would be low.

Independent culling Method

In the use of this method, selection may be practiced for two or more traits at a time, but for each trait a minimum standard is set that an animal must meet in order for it to be saved for breeding purposes. The failure to meet the minimum standard for anyone trait causes that animal to be rejected for breeding purposes.

The independent culling method of selection has been widely used in the past, especially in the selection of cattle for show purposes, where each animal must meet a standard of excellence for type and conformation regardless of its status for other economic traits. It is also used when a particular color or color pattern is required. It is still being used to a certain extent in the production of show cattle and in testing stations. It does have an important advantage over the tandem method in that selection is practiced for more than one trait at a time.

The Selection Index Method

This method involves the separate determination of the value for each of the traits selected for, and the addition of these values to give a total score for all of the traits. The animals with the highest total scores are then kept for breeding purposes. The influence of each trait on the final index is determined by how much weight that trait is given in relation to the other traits. The amount of weight given to each trait depends upon its relative economic value, since all traits are not equally important in this respect, and upon the heritability of each trait and the genetic associations among the traits.

The selection index is more efficient than the independent culling method, for it allows the individuals that are superior in some traits to be saved for breeding purposes even though they may be slightly deficient in one or more of the other traits. If an index is properly constructed, taking all factors into consideration it is a more efficient method of selection than either of the other two which have been discussed, because it should result in more genetic improvement for the time and effort expended in its use.

The kind of index used and the weight given to each of the traits is determined to a certain extent by the circumstances under which the animals are produced. Some indexes are used for selection between individuals, others for selection between the progeny of parents from different kinds of matings, such as line-crossing and crossbreeding, and still others for the selection between individuals based on the merit of their relatives, as in the case of dairy bulls, where the trait cannot be measured in that particular individual.