

Chapter One

LITERATURE REVIEW

1.1 - Introduction

Meat sheep is the most popular type of sheep being raised in the world. Considering the reports on crossbreeding by numerous researchers, and the promising pragmatic results, it is found to be a *prima facie*, powerful tool for meat production, especially in the meat sheep and poultry industries throughout the world. presently, there is an increasingly interest in crossing of mutton breeds over diverse sheep breeds, so that a large proportion of lamb in the commercial sectors of livestock production is produced in this way.

The main purpose of raising sheep in Iran in the first instance is to produce lamb and milk which are among the most popular animal products, possessing high nutritional values. Production of wool for manufacturing of the reputable Persian carpets and apparels is a further purpose. There is a wide range of different breeds and strains of sheep in Iran, providing the breeders with potentially rich genetic resources, in terms of a large variation in genetic material between the existing breeds. This is a valuable asset enabling the breeders to take advantage of crossbreeding gains which in most circumstances could be superior to gains from straightbreeding programs.

As distinct and specialized mutton breeds for crossbreeding are not available in all regions of Iran therefore, it is not always easy to decide which breeds are the best to cross, and this dilemma would be a subject of debate. In addition, even when such breeds are available, scrutiny

about the choice of breeds and economic consequences for a long period of time, as well as about the management parameters, would be of paramount importance. Management parameters in this regard mainly include type of the crossing system to adopt and its optimal population structure. By means of simulation modeling, breeders can most efficiently overcome the problems associated with the logistics of crossing systems. Therefore, to approach optimum and proficient crossing systems, employment of modern technologies such as breeding system modeling is deemed to be necessary especially for the commercial crossbred lamb producers. Accordingly, two optimum design crossbreeding computer models for the above purposes (only for self-contained flocks) will be introduced and discussed in this thesis. Basically, for the design and continuous improvement of crossbreeding models, a good knowledge of different crossing systems together with the relevant genetic principles is essential. In the following, these basic principles shall be offered, by reviewing different publications in this concern.

Crossbreeding in general

Crossbreeding and selection are the two major tools available to the animal breeder (Kingham, 1991). After "selection" crossbreeding is the second major method of exploiting genetic variation (Nicholas, 1987). It is an important tool available to animal breeders for achieving their basic aim being the development of genotypes that produce in greater quantities and/or more efficiently (Kingham, 1984). It follows that gains from selection and mating within breeds accumulate over generations, whereas those from crossbreeding appear immediately. Thus, crossbreeding provides the flexibility to react to changes in the production and marketing environments (Swan and Kinghorn, 1992).

Crossbreeding is the mating of animals from different breeds, in order to obtain progeny that outproduce their parents' average production with respect to quantity and/or quality of their products. Strictly speaking, according to Nicholas (1987), it can be defined as "the mating of animals from different populations which can be strains, breeds, or species", and is generally carried out between populations that have not intentionally been inbred, but which have been raised separately from each other for varying time periods. The resulting animals are referred to as crossbreds, being distinct from those produced within a population known as straightbreds. Crossing is widely applicable in animal production, so that most of the animals produced for meat are the progeny of a 3-way cross or a backcross (Falconer, 1989).

In essence, existing breeds or closed lines of different animal species are mildly inbred lines. The differences in mean gene frequencies, and degrees of homozygosity relative to a supposed population covering all crosses possible of breeds within a given species, determine the relative straightbreds' performance levels. The differences include average, dominance and non-allelic interactions of genes. Deliberate and natural selection, and random drift in gene frequencies and in the degree of heterozygosity (inbreeding) of populations have caused breed differences. Crosses of breeds or lines result in change in performance of the progeny, compared to that of the parents, from complementary maternal/paternal effects, and increased heterozygosity (reduced inbreeding) for dominant alleles. The performance change of offspring is due to changes in non-allelic interactions as well (Dickerson, 1993).

Crossbreeding has an initial consequence being an increment in heterozygosity in the offspring population. In crossing between breeds or other extensive crosses, a new combination of genes within and between loci which is an important outcome of such crosses, is developed (Turner, and Young, 1969).

Planning of crossbreeding programs needs a good knowledge of the genetic basis of heterosis. In addition to interaction within loci, namely dominance effect, there is a different sort of interaction between loci, called epistatic effect. When dominance is considered as a component of heterosis, heterozygosity with respect to breed of origin is taken into account. Epistasis can be classified in two general categories. First, interaction between single genes and total genotypes at all other loci, and is considered as a scale effect. And, the second, interaction within small groups of genes whose products are interdependent in function (Kinghorn, 1982).

Theoretically, in wide crosses of animals, recombination effects are expected to be present due to decomposition of desirable epistatic co-adapted gene complexes that exist in purebred populations and cannot be regarded as negligible. Epistatic recombination losses would account for non-linear relationships between the amount of heterosis expression and the degree of heterozygosity. Epistatic effects are considered to be responsible for the deviation of mean performance of F_2 generation from the expected mean based on F_1 compared to parental mean, in adult traits (Nitter, 1978). Of course, a halving in expression of breed dominance in F_2 animals must not be neglected.

Great effort is needed to evaluate the genetic constituents of breeds and their crosses accurately enough to predict the expected performance from differing choices of breeds and breeding strategies. The multiple-trait nature of breed differences and their interactions with production environments by which the economic efficiency of the livestock production-marketing system is determined, make the task more complicated (Dickerson, 1993).

Reports of systematic crossbreeding did not issue till the early 1900's, while the crossing of animals has contributed much to emerging of new breeds (Warwick and Legates, 1979). In systematic crossbreeding, new genes are entered into the population for specific purposes. Thus, it should not be mistaken with mongrelization which is quite different from the systematic crossbreeding (Hammond, 1963). In mongrelization, an animal's parents are the product of a mixture of different breeds that are crossed without a particular intention or enough care for the characteristics they possess. In contrast, the animals involved in systematic crossbreeding are usually selected from breeds having a long pedigree, and which correspondingly possessing a high quality of the desired characteristics.

No breed is superior in all traits in terms of prolificacy, fast gaining lambs, carcass grade etc. Generally speaking, commercial production of animals is seldom efficient when using only one breed. The pig and poultry industries have nearly entirely shifted towards crossbreeding. A large amount of mutton is produced through crossbreeding in the sheep industry, and in some countries beef is commonly produced by raising crossbred animals (Nitter, 1963). In the USA, an approximate 80% of market lambs, 80% of layers, 90% of market hogs, and 95% of broilers are crosses (Ensminger and Parker, 1986).

1.2 - Reasons for crossing of breeds

Today, there is a great interest in crossing of a diverse range of breeds and strains within species especially in commercial sectors of animal production. The reasons for the wide use of crossbreeding in commercial livestock production are as follows:

1) Exploitation of heterosis

One reason for the use of crossbreeding is to take advantage of heterosis that cannot be fixed within a line or breed (Lasley, 1972). The word

"heterosis" was coined by Shull in 1914, as Sheridan (1981) cited from Shull (1948). Heterosis is the amount of production of the crossbred progeny that exceeds the parents' average for a given trait. In the dominance model of heterosis, the total expression of heterosis consists of the direct individual, maternal, and paternal heterosis.

One important purpose of the employment of crossbreeding is to improve the progeny's fertility and growth. The benefits of crossbreeding come part from improving fertility of progeny by making use of heterosis in crossbred dams and part from combining different traits for which the lines have previously been selected (Falconer, 1989).

The ceaseless natural and artificial selection for desirable traits in different geographical and climatic locations in farm animals, has resulted in inbreeding and increased distinction between breeds and reduced population size. It follows that, changes in genotype frequencies and then in gene frequencies (due to recurrent selection within each breed population) in favor of desirable characteristics such as growth rate etc., has increased the resemblance by descent of allelic gene pairs (with non-additive effects). Neglecting the possible resemblance by origin (caused by genes with identical structural formulas without any relationship between parents), it has resulted (Falconer, 1989) in an increment in inbreeding depression for some desirable traits especially in fertility. By means of crossing, inbreeding depression on important traits of farm animals e.g. fertility, weaning rate, etc., can be lifted up through expression of heterosis in crossbred products.

Most classes of traits, especially ewe reproductive traits present favorable heterotic effects (Kingham and Atkins, 1987). The greatest expression of heterosis in traits is mostly associated with reproduction and viability (Nicholas, 1996), e.g., survival and growth rate to weaning which are expressed early in life. But, only a moderate amount of heterosis is expressed in feed-lot performance gain being measured after weaning. Also, heterosis seems to impact carcass quality of farm animals to a very little extent (Lasely, 1987).

Heterosis for traits related to fertility usually ranges between + 5% and 25%. For production rate, it is usually between -5% and 10% (Swan and Kinghorn, 1992). Garrett and Cole (1980) reported the heterosis of 13%, 10%, 2%, and 2% in first-cross sheep, and that of 38%, 17%, 17%, and 2% in three-breed cross sheep, expressed as percentages of the parental breed's average production for weaning weight per female bred, weaning weight per animal, number or percent weaned, and number or percent born, respectively.

As the effect of heterosis accumulates over traits in terms of direct and maternal expressions, it can be more valuable than this. For instance, as Swan and Kinghorn (1992) cited from Gregory and Cundiff (1980), for a composite trait like weight of calf weaned per cow joined, the crosses among *Bos taurus* cattle present an estimated amount of 23% heterosis, whereas it is expected to be up to 50% in *Bos taurus* × *Bos indicus* crosses. Traits having a high rate of heritability show a consistent response to selection but usually show little response to heterosis. In contrast, traits of low heritability such as mothering ability, lambing interval, and conception rate usually respond favorably to crossbreeding (Ensminger and Parker, 1986). Therefore the heterosis phenomenon is the best chance to improve lowly heritable traits, e.g. reproductive traits, birth weight and weaning weight. By deliberate use of ram and ewe breeds, crossbred dams would be capable of raising a remarkably increased number of heavier, viable rapid growing lambs per year as a result of direct and maternal heterosis.

In general, traits showing heterosis, also show inbreeding depression. It follows that inbreeding depression takes place where only the non-additive gene actions exist (Nicholas, 1996). Therefore, according to Falconer (1989, Chapter 14), heterosis phenomenon is simply inbreeding depression in reverse. The same author used an example supporting this idea.

The dominance model of heterosis says that in general, desirable genes dominate undesirable genes and heterosis is expressed linearly as a function of the extent of heterozygosity (Heamshaws and Barlow, 1983). As can be seen from the argument by Falconer (1989, Chapter 14), heterosis expression in a cross depends on the square of “difference in gene frequency y ” between breeds or populations, and the total amount of heterosis expressed in F_1 is sum of the dominance deviations d of those loci having different alleles in the lines or breeds involved in crossing. Equation 1 presents this concept:

$$H_{F_1} = \sum dy^2 \quad (\text{equation 1})$$

It follows that if a particular cross doesn't present heterosis it doesn't indicate the lack of dominance effects in the individual, as heterosis like inbreeding depends on directional dominance and the absence of heterosis might be due to the balance between opposite directions of heterotic effects i.e., some loci have dominance effects in one direction and some in the other, giving rise to no expression of heterosis.

With an increase in the genetic distance between two breeds, a proportional amount of heterosis will be expected in crossbred offspring (Ensminger and Parker, 1986; Nicholas, 1996). Moreover, with crossing breeds having larger genetic background differences a higher amount of heterosis should be obtained (Lasely, 1987) as heterotic effects accumulate over traits. Thus, when different breeds are crossed, a higher total amount of heterosis should be expressed across traits, compared with when crossing 2 lines from one breed. This can be illustrated another way by saying that the level of (allelic) heterozygosity between 2 purebred populations and crosses of them directly depends on the level of heterozygosity with respect to breed of origin of genes (Kinghorn, 1982).

Up to this stage, from the above argument we understand that the expression of heterosis depends on the degree of heterozygosity of parents in a cross. Now, we need to investigate whether the allelic heterozygosity is proportional to the degree of heterozygosity in regard to breed-of-origin. If so, then we conclude that the more distinct the parents involved in a cross, the greater would be the expression of heterosis. It follows that the simplest proof for this is that, as F_2 's are expected to be heterozygous at half of their loci, therefore they usually present half of F_1 heterosis, provided random mating among F_1 animals, to produce F_2 's possessing randomly associated genes. This idea will be tested in the following using an algebraic example with the assumptions made below. The logic adapted from Kinghorn (1993):

Genotype	A_1A_1	A_1A_2	A_2A_2
Frequency	p^2	$2pq$	q^2
Value	$+a$	d	$-a$

Assume there are 2 distinct breeds of straightbred sheep in 2 populations at equilibrium, symbolically shown as breed X and breed Y. The gene (allele) frequency of A_1 (conventionally, allele frequencies are called gene frequencies!) in breed-X population is assumed to be 0.6, and that of A_2 , 0.4. Thus, $p_x = 0.6$ and $q_x = 0.4$. Also, for breed-Y population $p_y = 0.2$ and $q_y = 0.8$. The value of genotype A_1A_1 is $+a$, and that for A_2A_2 equals $-a$. In the meantime, allele A_1 dominates allele A_2 when they join together in crossbred offspring. The possible genotypes in each purebred and or crossbred population will be A_1A_1 , A_1A_2 and A_2A_2 . The mean performance for each purebred population will be obtained in the following using the Hardy-Weinberg law:

Mean performance of breed X is:

$$(0.60p + 0.40q)^2 = 0.36p^2 + 2 \times 0.6 \times 0.4pq + 0.16q^2 = 0.36a + 0.48d \\ -0.16a = 0.20a + 0.48d.$$

These figures for breed Y are as follows:

$$(0.2p + 0.8q)^2 = 0.04p^2 + 2 \times 0.2 \times 0.8pq + 0.64q^2 = 0.04a + 0.32d \\ -0.64a = -0.60a + 0.32d.$$

The parental mean is then:

$$(0.20a + 0.48d - 0.60a + 0.32d) / 2 = -0.20a + 0.40d.$$

If these 2 populations of breeds X and Y are crossed, the genotype frequencies in the progeny will be the product:

$$(0.6p + 0.4q) \times (0.2p + 0.8q) = 0.12p^2 + 0.48pq + 0.08qp + 0.32q^2 \\ = 0.12p^2 + 0.56pq + 0.32q^2$$

The progeny's mean performance will then be:

$$0.12a + 0.56d - 0.32a = -0.20a + 0.56d.$$

The amount of heterosis is computed in the following:

$$-0.20a + 0.56d - (0.20a + 0.40d - 0.60a + 0.32d) / 2 = -0.40a + \underline{0.16d}$$

Now, we calculate the amount of heterosis for this single trait, based on the allelic gene frequencies using equation 1 above, to compare the results:

$$H_{F1} = dY^2 = d(0.6 - 0.2)^2 = \underline{0.16d}.$$

As can be seen, the heterosis amounts computed in both ways have equal values, confirming that the level of allelic heterozygosity between 2 purebred populations and crosses of them directly depends on the level of heterozygosity with respect to breed-of-origin of genes, and the more distinct the breeds in a cross, the greater the expression of heterosis.

This principle is valid For a F_2 population as well. To calculate the amount of heterosis in F_2 , we first need the frequencies of alleles concerned in F_1 's. It is obtained by averaging the parental frequencies:

$$(0.6p_x + 0.2p_y) / 2 = 0.4 \text{ for } p_{F1} \text{ and:}$$

$$(0.4q_x + 0.8q_y) / 2 = 0.6 \text{ for } q_{F_1}$$

The F_2 mean performance will be the product:

$$(0.4p_{F_1} + 0.6q_{F_1}) \times (0.4p_{F_1} + 0.6q_{F_1}) = 0.16p^2 + 0.24pq + 0.24qp + 0.36q^2 = 0.16a + 0.48d - 0.36a = -0.20a + 0.48d.$$

As the parental (F_1) mean is $-0.20a + 0.56d$, therefore, the heterosis in F_2 will be $0.56d - 0.48d = 0.08d$, half the amount of that in F_1 . This is because, here, the breed-of-origin heterozygosity is $1/2$, resulting in a halving in the expression of heterosis, compared with that in F_1 , where the breed-of-origin heterozygosity is 1. This assumption will also be made while computing the amount of heterosis expression in various crossbred-type animals in the crossbreeding models which will be introduced later in this thesis.

We can now draw a general conclusion that, the amount of heterosis expressed in a cross depends on the difference in the degree of heterozygosity of parental breeds, appeared in two possible ways as follows: 1) due to changes in genotype frequencies (with same gene frequencies) of 2 populations i.e., 2 lines from one breed, originating from one base population in absence of selection, and 2) due to the changes in gene frequencies (breed difference) of 2 parental populations as a result of natural and artificial selection as well as of migration, random drift and mutation etc, as it is the case in distinct breeds of various species of animals. This has caused the genetic diversity of breeds, resulting in heterotic effects i.e. the heterosis phenomenon in crossbreeding.

However, it must be emphasized that the expected relationship between the degree of heterozygosity and heterosis is not always linear, e.g. in F_2 crossbreds. As mentioned earlier, this non-linear relationship is believed to be due to the epistatic recombination loss in crossbred F_1 progeny which changes their gene complexes that have additive effects. This, in turn causes change in the trend of heterosis expression, in some instances.

Factors affecting the expression of heterosis are as follows. These factors are discussed in detail by Johnston (1988).

- 1) diversity of breeds.
- 2) degree of heterozygosity.
- 3) epistasis.

- 4) reciprocal differences i.e., which breed should be used as sires and which one as dams to attain more heterosis.
- 5) dam age and parity.
- 6) heterosis x environment interactions, e. g., in poorer environments, generally a higher amount of heterosis is expressed.
- 7) fitness (adaptation to environmental stresses).
- 8) age and sex.

As a general rule, for crossing of breeds, those must be chosen that are superior in highly heritable characteristics, being mostly controlled by the additive gene effects and those having superior combining ability to express more heterosis. Thus, purebred breeders should improve the highly heritable traits within the purebreds. The improved breeds can then be crossed to take advantage of heterosis in traits that express it (Lasley, 1972).

Nonetheless, in crossbreeding systems, breeds or strains should be under selection for continued improvement of those traits that are high in heritability and low in heterosis expression (Barker, 1994).

Also, because to the breeder, maximizing overall efficiency of the production system is desirable, combining various breeds in such a way that facilitates achieving this goal is important. So, the breeder can benefit from the improvements gained by use of both of the major tools, namely selection and crossbreeding. Application of these tools, results in an increased production level through the utilization of additive breed effects, and non-additive gene effects (heterosis) respectively.

2) The use of complementary effects of sire and dam

Complementarity is (largely due to) exploitation of additive genetic differences between breeds (Insminger and Parker, 1986). It refers to the advantage of a cross in which the parents are genetically different from each other but have complementary attributes for producing a more desirable offspring.

For an aggregate trait, the degree of complementarity depends on the extent of interaction between reciprocal crosses or among crosses of different breeds. Heterotic effects play only a small role in complementarity but reciprocal advantage in complementarity is evident. Also, complementarity has a genetic and an environmental component (Cartwright, 1969) which the latter is usually disregarded.

Although it may be expressed for some traits, heterosis is not usually accounted for, when complementarity of sire and dam is discussed. But, besides the above author who suggested a small heterotic component for complementarity, Nitter (1978) referred to complementarity as the *sire-dam heterosis*. As he reported, Moav (1966) too applied this definition for complementarity.

In meat sheep crossbreeding, rams and ewes do not equally contribute to the performance of the progeny. Consequently the breeds of sheep are categorized into ewe breeds and ram breeds. Ewe breeds are selected for adaptability to environmental conditions, reproductive efficiency, wool production, size, milking ability and longevity. Ram breeds are meat-type or crosses of two of them. They are selected for growth rate and carcass qualities and are used for crossing on ewe breeds (Ensminger and Parker, 1986).

Let's assume 2 breeds of sheep, one good in prolificacy and the other good in growth rate. If these ewes and rams are crossed, then the complementarity would occur as the resultant offspring are, on average, heavier than those produced when using either of the purebreds. This is true even when disregarding improvement of fertility due to heterosis. The argument is that as a larger number of more rapidly growing lambs are raised by the prolific dams thus, at slaughter age, the amount of the salable lamb is notably larger compared with that in a straightbreeding program.

Fast growing lambs reach the same weight in a shorter period of time, compared with those having a slower growth rate. Thus, the former are leaner, as fatness is a late-developing character. Accordingly, in the meat production industry, there is the need of fast growing animals in large scales to answer the market demands. This is achieved by use of two lines of animals (usually different breeds) to produce F_1 dams having good fertility. These crossbred females are crossed with sires from a third line that have good growth rate. If a suitable third line is not available, F_1 animals are backcrossed to one line of the parental lines. The improvement in the growth rate of the progeny comes from heterosis and

additive effects (complementary effects) of the sire line. The progeny may not always have a good growth rate as their best parental line, but as the fertile crossbred mothers produce a larger number of progeny, the crossbreeding will be economically profitable (Falconer, 1989). This concept is illustrated more clearly in Table 1.

Table 1. Results obtained from a 3-way cross of sheep breeds serve to illustrate the complementary effect of sire and dam in sheep, excerpted from Falconer (1989): *a*) fertility as the number of lambs weaned per ewe mated; *b*) growth rate as the weight per lamb at weaning; *c*) the economically important trait, total weight of lambs weaned per ewe mated, being the product (*a*) x (*b*). As can be seen, weaning weight of the 3-way cross (A x B) x C was not as good as the best breed i.e. breed C, but due to the increased number of lambs produced, the total weight of lambs weaned was 18% higher than the best pure breed C. This superiority in performance comes from combining the superiority of growth of the sires from breed C, with heterosis of fertility from the crossbred dams, (A x B)'s.

	Production per ewe mated		
	(a) No. of lambs weaned	(b) Weaning weight (Kg) per lamb	(c) Total weight (Kg) weaned
<i>Pure breeds:</i>			
A = Shropshire	0.80	23	18.4
B = Southdown	0.79	19.1	15.1
C = Hampshire	1.00	29.2	29.2
Mid-parent (1/4 A + 1/4 B + 1/2 C)	0.90	25.1	22.6
3-way cross (A x B) x C:	1.25	27.5	34.4
Heterosis, % above mid-parent	39	10	52
Superiority over the best breed (%)	+25	-6	+18

* = $((C + A) / 2 + (C + B) / 2) / 2$ (annotation from the present author).

Even when there is a simple crossbreeding on which a large breed of sire is mated to a fertile and reasonably small breed of dam, complementarity of sire and dam occurs. According to Kinghorn (1993), in this case the proportion of feed used for growing offspring is increased (more meat is produced) and consequently the enterprise benefits economically. This can be justified even we assume that the cost of the extra amount of feed (per unit salable meat) consumed by crossbred offspring is not lower than that of purebreds. Further, the reduced dam costs per unit of lamb produced in the enterprise is additional advantage. This advantage is due to the utilization of small dams having lower costs compared with larger dams.

In other words, in crossbreeding, the sire and dam breeds' feed intake complement each other, and increase the biological efficiency of the production system. In a breeding system the maintenance costs of breeding females can incur a high proportion of the total costs, particularly when their fecundity is low (Swan and Kinghorn, 1992). Food costs consist of about 70% of total costs in a meat sheep production system. A reduction in the food costs will result in a large increase in the biological efficiency of the production system. In purebreeding enterprises, increasing mature size can increase the biological efficiency of the production system to a certain degree. This is because a higher amount of meat per dam is produced, by way of increased weight of the offspring with the same dam costs mainly including feed costs.

When, for instance, in a meat production system a large-mature-size sire breed is mated to a small-mature-size dam breed, the proportion of food for maintaining the dam, relative to (the number of or weight of) its offspring will markedly decline and as a consequence, the biological efficiency of meat production increases (Thompson, 1991).

The same author reported that using a first-cross production system with sires and dams (for utilizing complementary effects) differing in mature size by 30%, resulted in 7% increase in biological efficiency which was about twice that gained from increasing mature size by the same proportion in a purebred enterprise. This was due to 15% increase in mature size of offspring, which effectively increased lean meat production while having the same maternal costs in the system. Moreover, a second-cross system, benefiting from complementary effects and increased fertility of the first cross dams presented almost 18% increase in biological efficiency in comparison with a purebred production system. The cause of this increase was a greater output for the same maternal cost resulting from a 15% increase in mature size of the progeny relative to the dam and from a 25% increase in weaning percentage.

3) Averaging of breed effects

Crossing exploits differences in average additive gene effects (Nicholas, 1987). This can be achieved where an animal of intermediate size is needed to meet a special pasture cycle or market demand (Kinghorn, 1993). For instance, some markets might need carcasses of cut size and fat cover intermediate to parent breeds (Swan and Kinghorn, 1992).

The manipulation of the carcass composition is possible by use of the average effects of breeds through crossing large-mature-size sires on smaller dams. There is little heterosis for carcass traits after adjustment for the stage of maturity, but the carcass quality can be improved by increment in the mature size of the offspring, when a large-mature-size sire is crossed on a smaller dam. The crossbred progeny's mature size will be the average of that of their parents, plus a certain amount of heterosis expressed. Thus, crossbred progeny with the same slaughter weight, are at a lower stage of maturity, compared with those bred in a purebred flock. It follows that as the differences in carcass composition would be a function of the differences in the stage of maturity, the crossbred progeny that are younger at the same weight at slaughter, are thus leaner than purebred offspring (Thompson, 1991).

4) The possibility of widest use of genetic resources

This includes the possibility of increasing the selection intensity and reducing the rate of inbreeding (Kinghorn, 1993). Crossbreeding provides the breeder with a greater flexibility in determination and development of an efficient breeding program as there will be a wider range of genetic material in comparison with when using only one breed. Therefore, more intense selections can be applied while highly avoiding inbreeding problems (Swan and Kinghorn, 1992).

1.3 - Systems of crossbreeding

There are several systems of crossbreeding which shall be discussed in the following. The major crossbreeding systems can be classified into three:

- 1) Specific crossing systems*
- 2) Rotational crossing systems.*
- 3) Synthetic or composite crossing systems*

Specific crossing systems

Specific crossing systems include upgrading, two-breed crosses or first crosses, three-breed crosses, and four-breed crosses.

1) upgrading

In upgrading, successive back-crosses of selected female offspring with a superior male parent are carried out for a number of generations in order to introduce a new gene or special genes to a given population.

This also can be done to replace one population with the other, for instance, local population (Nicholas, 1987). This system uses straightbred parental lines at the commencement of the program, and then female animals are mated to unrelated sires from the imported lines (Ensminger and Parker, 1986). Consequently, the resultant progeny benefit from both direct and maternal heterosis. Once introducing genetic material is completed, the offspring are mated to the existing upgraded breed (Swan and Kinghorn, 1992), but at this stage, the expression of heterosis ranges between zero and a definite level, depending on the proportion of the new genes in the population i.e. the degree of breed heterozygosity of the existing breed. By outcrossing and backcrossing, a rapid and sure way of spreading the superiority of the imported breeds is feasible compared with when only successive selection within local breeds is carried out. However, using this method leads to a performance level of upgraded progeny equal to that of superior purebreds acquired by continuous selection (Dickerson, 1969).

It must be emphasized that continual backcrossing is not only unnecessary, but it also could be undesirable. It eliminates all of the useful local genes which could be utilized in the new breed being developed and finally results in replicas of the migrant animals that were alive 15 or 20 years ago. Therefore, the new breed would not have good adaptation to the local environment as the local breed has. If pure breeders carry out only one backcrossing (i.e., two stages of up-grading) or continue backcrossing of offspring at most, up to the 2nd generation (produce up-graded offspring from F_2 's), and then practice selection for desirable traits among the up-graded progeny, they would improve economically important traits more rapidly than by continual up-grading only. Consequently, an optimum proportion of the desired genes will exist in a particular production system. In substituting one population for the other, there will be variation in terms of the proportion of local and migrant genes among progeny of all subsequent generations, except for the first generation F_1 being half-bred (Nicholas, 1996).

Therefore, from the argument by the above-named author it can be seen that a spectrum of different types of gametes is formed in the up-graded progeny as a result of segregation and recombination during the formation of gametes in F_1 's and in all of the following up-graded

generations. Accordingly, in this spectrum, a gamete could be carrying genes from the imported breed ranging from 50% to 100%, for all of the generations except for the first one. That is why the breeder cannot be sure about the actual proportion of the migrant genes in a single individual. But, for an up-graded population with a statistically large enough size one can say that, on average, it possesses a certain proportion of migrant genes, depending on the number of backcrosses to a migrant breed carried out. Table 2 shows the proportion of a migrant breed in an up-grading procedure for 5 generations.

Table 2. Average proportions and the possible variation of migrant genes in an individual or in a population, in grading-up to a more desirable breed, from any local animals "L", e.g., for breed substitution. Source: Nicholas (1996).

Generation	Mating program	Designation (grade) of animals in square brackets	proportion of migrant genes in animals in square brackets		
			Min. ¹	Av.	Max. ¹
0	L x M				
	↓				
1	(LM x M)	1/2 [breed]	1/2	1/2	1/2
	↓				
2	((LM)M)xM	3/4 [breed]	1/2	3/4	1
	↓				
3	((((LM)M)M)xM)	7/8 [breed]	1/2	7/8	1
	↓				
4	(((((LM)M)M)M)xM)	15/16 [breed]	1/2	15/16	1
	↓				
5	etc.	31/32 [breed]	1/2	31/32	1

¹ Assuming no crossing-over.

2) Two-breed crossing systems

The two-breed crossing systems involve the mating of the sire and dam lines of straightbred animals. Offspring produced in this system are 100% heterozygous, and the direct heterosis is fully expressed. Also, breed effects such as complementary and the additive effects of genes are exploited in the progeny. This type of crossing is mostly advantageous where female animals are well adapted to specific environmental conditions, but there is the need of inheritance from animals that are efficient for feedlot and slaughter purposes (Warwick and Legates, 1979). For replacement of females in a 2-breed crossing system there will be two

options; purchasing the replacement females from outside the flock or replacing the old females with the best performing purebred females in the flock.

The second choice has the advantage of the female animals having been acclimatized to the environment of the existing farm. However, it has a disadvantage, the farm cannot have crossbred progeny from all matings when purebred replacement females are being produced (Lasley, 1972). In addition, this system has another disadvantage being the raising of two populations of purebred animals to use as sire and dam lines. Meanwhile, the system does not take advantage of the maternal/paternal heterosis.

3) *Three-breed crossing systems*

These systems are also referred to as three-breed terminal sire or three-breed specific (or static) crossing systems. In the three-breed special crossing systems, females of a breed that is excellent in maternal performance are mated to sires of a third breed that transfers the best individual performance in regard to production efficiency, to the progeny (Moav and Hi, 1966). For instance, breeds A and B which are well-performed in maternal traits, are crossed to produce (AB) progeny. Then, the best offspring are selected, and mated to the sires from breed C which usually is called terminal sire, having good carcass quality and growth rate. All of the (ABC) progeny are slaughtered. These systems benefit from 100% individual heterosis in crossbred F_1 's, as well as from 100% individual heterosis, 100% maternal heterosis, and from the breed effects and complementarity of sire and dam in F_2 's.



The three-way crossings are extensively used in the poultry industry. One disadvantage of these systems is that four separate lines of animals i.e., 3 straightbred lines representative for 3 breeds and one F_1 dam line, are needed unless the crossbred dams are bought in, in which case, only one sire line and one crossbred dam line should be kept in the flock. Therefore, in these systems management problems exist, especially in small flocks, in terms of providing female replacements either by purchasing or by producing in the flock, etc. In case of the latter, producing purebred dams reduces the number of crossbred progeny produced in the flock.

The possible unavailability of desirable breeds for use in this system could be a further obstruction for establishment of such crossing systems in some particular situations.

4) Four-breed crossing systems

Four-breed (or four-way) crossing systems involve the crossing of 4 lines of purebred animals plus two crossbred F_1 and one F_2 populations, and often are used in large, intensive livestock production units. These systems are applicable where the paternal heterosis is important as well (Kinghorn, 1993). Breeds A and B, being superior in carcass quality and growth rate are mated in the paternal flock to produce paternal sire line, and breeds C and D which have been chosen for excellency in maternal characteristics are mated to provide dams for maternal line. Then the selected superior sires from the paternal line and the selected dams from the maternal line are crossed to produce the commercial progeny. For better results, usually many test crossings are carried out to find the best combining ability for sire and dam lines. Table 3 provides a general understanding of four-breed crossing systems. As can be seen, these systems take the full advantage of direct heterosis as well as of sire-dam complementarity in maternal and paternal lines. Meanwhile, in the final progeny, direct, paternal and maternal heterosis, as well as breed effects and complementarity of sire and dam are exploited.

Table 3. A simplified example of a four-way crossing system.

<u>Paternal line</u>		<u>Maternal line</u>	<u>Heterosis</u>	<u>Complementarity</u>
A x B		C x D		
↓		↓		
F_1	(AB)	x	Direct	Yes
	↓	(CD)		
F_2	(ABCD)		Direct + Maternal + Paternal	Yes

Four-breed crossing is occasionally used in domestic animals except in poultry industry where several breeding organizations use this system regularly. The actual amount of individual heterosis in the commercial offspring may not be the same as that in either of the parental F_1 lines (Nicholas, 1987). This is simply because there are 2 different types of parents involved in the first and second crossing procedures.

The greatest difficulty in establishing these types of systems is unavailability of 4 superior and profitable breeds or strains to keep in 4 different lines, plus the complication of the system and the need of a perfect management and relatively large investment.

Rotational crossing systems

Rotational crossing is another kind of crossing in which the sires of two or more breeds are mated to dams of the previous generation in sequence. This type of crossing system is sometimes referred to as crisscrossing or backcrossing system. The commonest systems of this type of crossing are 2- or 3- breed rotational crossing systems.

Advantages and disadvantages of rotational crossing systems

Rotational crossing overcomes some of the difficulties that exist in specific crossing such as obtaining all or some of the male and female replacements from outside the flock, because crossbred dams are self-replacing. This is an advantage, especially where management and disease problems exist (Swan and Knghorn, 1992), as well as where the unavailability of desirable replacements from outside the flock is known as a handicap (Nicholas, 1987). Rotational crossing systems use much of the potential heterozygosity, and the recombination loss is relatively low. The main disadvantage of rotational crossing is that they can't exploit different genotypes for individual and maternal performance (Hammond, 1994). Thus, it doesn't allow any (regular) exploitation of complementarity, as the crossbred populations can not be used only for one purpose like that in specific crossbreeding systems. Owing to this problem, rotational crossing is mostly advocated where the populations available for crossing show little or no complementarity, but express some heterosis being economically valuable (Nicholas, 1987).

However, a controversy may arise in saying that, in fact, there is some use of complementary effects in rotational crossing as a higher proportion of sire genes in the progeny in each generation results in complementarity, at least for one sire, but with a lower magnitude in comparison with a static 2-way or 2-way terminal crossing system. This complementarity fluctuates dramatically from one generation to another, due to changes in proportions of sire genes in offspring. Some scientists implicitly agree with this matter, for instance, Cartwright (1969) pointed out that rotational crossing systems benefit from heterosis but at the price of highly sacrificing of complementary advantages.

Meanwhile, in rotational crossing the breed composition varies to a high extent from one generation to another. Figure 1 presents the fluctuation in gene proportions of different breeds in crossbred animals, in a 3-breed traditional rotational crossing.

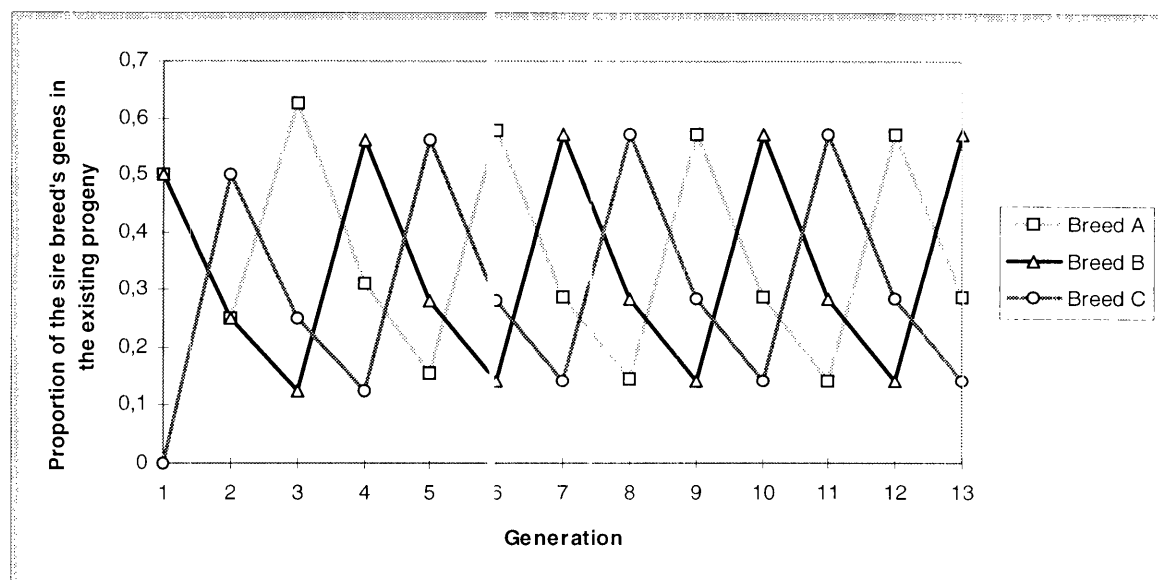


Figure 1. Oscillation in breeds' gene contribution to the progeny in a 3-breed traditional rotational crossing with sire rotation order of A-C-A-B-C-A-B... i.e., fathers of the progeny in generation 1 are sires from breed A, mated to purebred B dams in generation 0, then sires from breed C to (AB)'s (F_1 dams) in generation 1, etc. More details in this concern shall be offered in *3-breed rotational crossing systems* later in this Chapter.

This is a potential management problem and contributes to increased dystocia, inappropriate allocation of feed and reduced uniformity of product (Bennett, 1987). In case of the latter problem, breeders may have to use similar breeds for marketing and management purposes, and this results in a reduction in breed effects and complementarity. Another disadvantage of these systems is that, a large number of crossbred types is formed prior to reaching the system an equilibrium (Swan and Kinghorn, 1992).

Classification of the rotational crossing systems

1) 2-breed rotational crossing systems

In the 2-breed rotational crossing, for instance, dams from breed B are mated to sires from breed A in generation 0 to produce F_1 's in the 1st generation. Then the selected first cross females are crossed with sires from breed B and the dams from the 2nd generation are mated to the sires from breed A, etc. This procedure continues so that the selected females from within the flock are alternately mated to the sires from each breed. After several generations, the system reaches an equilibrium at which stage, the gene proportions from each breed will be two thirds from the immediate sire breed and one third from the other sire breed, as illustrated in Table 4.

Table 4. Proportions of genes from each breed together with the heterosis expression in the early generations at equilibrium in a 2-breed traditional rotational crossing system. Data from Nicholas (1996).

Generation	0	1	2	3	...	eqib.*	eqib.+ 1	eqib.+ 2
Sire breed mated to the dams below	A	B	A	B	...	B	A	B
	x	x	x	x	x	x	x	x
Dams & progeny	B	(AB)	(BAB)	ABAB	...	(A...)	(B...)	(A...)
	L→	L→	L→	L→	L→	L→	L→	L→
Breed's gene contribution A	0	1/2	1/4	5/8	...	2/3	1/3	2/3
B	1	1/2	3/4	3/8	...	1/3	2/3	1/3
Heterosis**	0	1	1/2	3/4	...	2/3	2/3	2/3

* = Generation at equilibrium.

** Heterosis expression is proportional to the average heterozygosity of progeny, relative to a first-cross individual, in a dominance model.

The amount of the heterosis exploited in an established rotation with n breeds contributing equally, under a dominance model (Kingham, 1993) is:

$$H_n = (2^n - 2) / (2^n - 1) \quad (\text{equation 2})$$

Where n is number of the breeds contributing to the rotational crossing and H_n the heterosis expressed for a n -breed rotational cross. Heterosis expression for this system would be $2/3$ of F_1 heterosis for $n = 2$. As Warwick and Legates (1979) reported, Carmon *et al.* (1956) proposed a formula to predict the performance of progeny in crisscrossing (2-breed rotational crossing) from the performance of the single crosses and the paternal breeds or strains. It is presented as follows:

$$R_2 = C_2 - (C_2 - P_2) / 3 \quad (\text{equation 3})$$

where R_2 is performance of a 2-breed rotation, and C_2 and P_2 are the performance of the single cross and the average performance of the two paternal breeds respectively. As can be seen from equation 3, the reduction in production level of a single cross is $1/3$ of the heterosis in a two-breed crossing which is in line with the previous computation of heterosis for a 2-breed rotational crossing.

2) 3-breed rotational crossing systems

The three-breed rotational crossing is quite similar to the two-breed rotational crossing, and uses three different sire breeds rather than two. After mating all the three sires to the selected crossbred females from within the population, the offspring will have (Warwick and Legates, 1979) 57% (4/7) of their genes from the breed of their immediate sire. The related formula (from the same source) is as follows:

$$S_n = 50 \times 2^n / (2^n - 1) \quad (\text{equation 4})$$

where n represents number of the breeds involved in a rotation and S_n percentage of genes from the immediate sire breed in a n -breed rotation. It follows that 29% (2/7) of genes will be from the breed of their second sire (paternal grand sire), and 14% (1/7) from the third breed. Tables 5 and 6 present these proportions and additional other details of 3-breed traditional rotational crossing systems. Also, as can be seen in Table 6, these systems almost reach an equilibrium in generation 6, but with a higher precision, equilibrium occurs in generation 14 or later.

Table 5. Proportions of genes from each breed together with the heterosis expression in the early generations at equilibrium in a 3-breed traditional rotational crossing system. Data excerpted from Nicholas (1996) and Cartwright (1969).

Generation	0	1	2	3	4	5	...	eqlb.*	eqlb. + 1	eqlb. + 2
Sire breed mated to the dams below	A	C	A	B	C	A	...	A	B	C
	x	x	x	x	x	x	x	x	x	x
Dams & progeny	B	(AB)	(CAB)	(AC/B)	(BACAB)	(CBACAB)	...	(C...)	(A...)	(B...)
	L→	L→	L→	L→	L→	L→	L→	L→	L→	L→
Prop. of each breed's genes										
A	0.00	1/2	1/4	5/8	5/16	5/32	..	1/7	4/7	2/7
B	1.00	1/2	1/4	1/8	9/16	9/32	..	2/7	1/7	4/7
C	0.00	0.00	1/2	1/4	1/8	9/16	..	4/7	2/7	1/7
Heterosis**	0.00	1.00	1.00	0.75	0.875	0.875	..	0.857	0.857	0.857

* = Generation at equilibrium.

** Heterosis expression is proportional to the average heterozygosity of progeny relative to a first-cross individual, in a dominance model.

Table 6. Details of a 3-breed traditional rotational crossing. The progeny in each generation are dams of progeny in the next generation. The procedure commences with A x B crossing, then continuous with C x (AB), A x (...), B x (...), etc. The progeny in generation 14 possess genes, 0.5714 (in absence of crossing-over) of which coming from sire-breed C.

Generation	Sire breed used	Proportion of the breed's genes in the progeny		
0	A	A	B	C
1	C	0.5000	0.5000	0.0000
2	A	0.2500	0.2500	0.5000
3	B	0.6250	0.1250	0.2500
4	C	0.3125	0.5625	0.1250
5	A	0.1563	0.2813	0.5625
6	B	0.5781	0.1406	0.2813
7	C	0.2891	0.5703	0.1406
8	A	0.1445	0.2852	0.5703
9	B	0.5723	0.1426	0.2852
10	C	0.2861	0.5713	0.1426
11	A	0.1431	0.2856	0.5713
12	B	0.5715	0.1428	0.2856
13	C	0.2858	0.5714	0.1428
14	A	0.1429	0.2857	0.5714
15	B	0.5714	0.1429	0.2857
16	C	0.2857	0.5714	0.1429
17	A	0.1429	0.2857	0.5714
18	B	0.5714	0.1429	0.2857
19	C	0.2857	0.5714	0.1429
20	A	0.1429	0.2857	0.5714
21	B	0.5714	0.1429	0.2857
22	C	0.2857	0.5714	0.1429
23	A	0.1429	0.2857	0.5714
24	B	0.5714	0.1429	0.2857
25	C	0.2857	0.5714	0.1429
26	A	0.1429	0.2857	0.5714
27	B	0.5714	0.1429	0.2857
28	C	0.2857	0.5714	0.1429
29	A	0.1429	0.2857	0.5714
30	B	0.5714	0.1429	0.2857

The heterosis expressed is $\frac{6}{7}$ in this type of crossing. The above authors also quoted a formula from Carmon *et al.* (1956) to predict the performance level of 3-breed rotational crossings. The formula is presented in the following:

$$R_3 = C_3 - (C_3 - P_3) / 7 \quad (\text{equation 5})$$

where C_3 stands for the average performance of three single crosses possible among three breeds and P_3 for the average performance of the

three parental breeds. The reduction in heterosis is $\frac{1}{7}$ of the average heterosis for three possible single crosses.

Therefore, in a 3-breed rotational crossing only about $\frac{1}{7}$ of the maximum average maternal and individual heterozygosity is lost, but further loss in maternal and individual performance could be due to inter-breed recombination in gametes (Dickerson, 1969).

Synthetic crossing systems

Crossbreeding can also be used to form synthetic breeds or composites. The foundation of new breeds based on crossing is a time-worn technique (Dickerson, 1969). No current breed has a specific combination of favorable traits for a particular production-marketing system, e.g., growth potential and parasite resistance. This is one of the main reasons for developing new breeds. Synthetic breeds are developed where genetic variation is necessary to be increased to select within the population with the highest intensity possible and to benefit from reversing inbreeding depression and from heterosis expression as well (Sandy McClintock, 1982; Nicholas, 1987), in addition to complementary and additive effects of desirable gene complex.

Probably, complementarity in general is the main feature of synthetics, being achieved either in the earlier stages of crossing or after a number of generations, both along with selection. Therefore, when this process is over, a long-lasting optimum proportion of the traits completing each other, making the whole genotype a favorable blend, has already been attained. That is why the choice of breeds contributing to a new single breed should be carefully weighed up before uptaking this type of crossbreeding system. However, if we look at synthetics from the standpoint of continual possibility of utilization of complementary effects of terminal-sire and dam after formation of these populations, according to Dickerson (1993), synthetics alone, are unable to benefit from this phenomenon.

After establishing the desirable breeds, synthetics can be kept in the production system to be propagated (as straightbreds), or further improved, possibly by continual mating of dams only to F_1 crossbred sires from the breeds contributing to the origination of the existing synthetic (Dickerson, 1993).

In general, the amount of heterosis expression (for any type of synthetics) at equilibrium i.e., once well mixed is as follows (Kinghorn, 1993):

$$H_{syn.} = H_{F_1} (1 - p^2 - q^2 - r^2) \quad (\text{equation 6})$$

where $H_{syn.}$ stands for the amount of heterosis expressed in a F_2 synthetic, provided F_2 and the following generations result from matings within F_1 's, and p , q , and r , proportions of the 3 breeds involved.

For balanced synthetics (with equal contribution of genes from each breed), we can use the following simpler formula from the same author:

$$H_{bal.} = H_{F_1} (n - 1) / n \quad (\text{equation 7})$$

where $H_{bal.}$ represents the amount of heterosis in a balanced synthetic, H_{F_1} F_1 heterosis, and n number of the parental breeds used to establish the synthetic.

All the equations 1-7 are necessarily presented differently from the original formulas in the references, with respect to some additional symbols used in this concern.

Optimal contribution (optimum utilization of complementary effect) of each breed in synthetics can be attained by way of increasing additive value to result maximum performance level, but at the cost of some reduction in heterosis expression (Kinghorn, 1993).

As an example, excerpting from the same source, in a 3-breed optimum synthetic with gene proportions of 0.57, 0.31, 0.12 from 3 breeds, expression of heterosis declines from 0.67 in a balanced synthetic to 0.56, here. This can be seen from the following calculations, using equation 6:

$$H_{(optimum)} = H_{F_1} (1 - 0.57^2 - 0.31^2 - 0.12^2) = 0.56 H_{F_1}.$$

It must be noted that in this case, due to the optimized proportion of each breed contributing to a synthetic, and accordingly, the maximized additive effects of genes, the total merit of the synthetic breed could be higher, although benefiting from less expression of heterosis, compared with a 3-breed balanced synthetic with equal gene proportions for each breed.

For an optimum synthetic, both within- and between-breed effects should be considered. Hence, a nearly optimal proportion of each breed is obtained by balancing the value of increased heterosis against contributing more breeds which might be inferior (Swan and Kinghorn, 1992).

Advantages and disadvantages of synthetic crossing systems

Only one versatile synthetic flock could be sufficient for a particular production-marketing system with much less complicated logistics compared with other crossing systems employed to reach the same breeding objectives, as here only one uniform population of animals exists.

Synthetic breeds are suitable for small flocks or herds in order to avoid the management problems of specific and rotational crossing systems in terms of mating systems and the variability of the breeds used (Swan and Kinghorn, 1992). Synthetic breeds do not require replacements from purebred parental lines, selection can be applied to them more directly and rapidly, and they can be used as specialized parental breed lines in specific two-breed crossing systems. Therefore, they can also contribute to some increment in heterosis in maternal and/or paternal performance, to the complementary effect of terminal sire and dam, and to reducing the proportion of matings in parental lines (Dickerson, 1993; 1969).

Compared with the parental breeds, while disregarding the subsequent possible decrease in genetic variance through early inbreeding (via intense within-population selection) in synthetics, they have a higher initial heterozygosity, and thus, a higher initial performance level would be presented at the commencement as composite breeds. Accordingly, even when heterosis is important (assuming no initial inbreeding depression), new breeds can be developed, especially when management conditions and breeding objectives are variable, or when in some countries or areas a simple breeding program is necessary (Dickerson, 1969).

But, in comparison with 3-breed specific or rotational crossings, synthetics have generally a lower genetic potential for commercial performance because of the following reasons (Dickerson, 1969; Hammond, 1994):

- 1) in synthetic breeds the proportion of heterozygosity is lower in comparison with specific or rotational crossing systems. Therefore, they show only some of the individual and parental heterosis. For instance, in a 3-breed synthetic, heterosis is $2/3$ versus 1 and $6/7$ in specific and

rotational crossing systems, respectively, with the same number of breeds.

- 2) synthetics are unable to exploit breed differences in maternal versus individual performance, as they don't allow making use of different genotypes for male and parents.
- 3) synthetics show maximum inter-breed recombination (epistatic) loss which is potentially greater than that in systematic crossings mentioned earlier. This phenomenon causes a certain loss in favorable joint effects of non-allelic genes fixed in parental breeds by means of selection.

The mating of crossbreds to crossbreds eventually results in a remarkable variation in the progeny followed by lack of uniformity in some traits, one reputed of which being coat color (Lasley, 1987). Therefore, there will be a relatively high degree of variation in additive genes responsible for the desirable traits. However, this inconsistency can be avoided by way of continuous selection for favorable attributes in synthetic populations while being in the process of establishment.

Further exploitation of synthetic breeds

As said earlier, synthetics take less advantage of heterotic effects i.e. less heterosis expression in comparison with specific and rotational crossing systems using same breeds. Swan and Kinghorn (1992) proposed crossing of a terminal sire breed on older synthetic dams, to take advantage of the increased heterosis in the progeny. The aforementioned authors also agreed with the idea of a sire-breed rotation in some sequence, using synthetic dams while their pedigrees are ignored, as proposed by Fennet (1987). They postulated that by optimizing the rotation order and optimizing female culling age, more heterosis can be expressed in such crossing system than in similar synthetics.

Modified systems of rotational crossing

There are several forms of modified rotational crossing systems. In conventional rotations, sire breeds are used equally and continuously, and the number of animals in each crossbred generation is assumed to be stable (Nitter, 1993), whereas in modified systems of rotational crossing there are some changes in this relation.

1) Rotational crossbreeding with generation preference

Another variation of rotational crossing is a system which is called *rotational crossing with **generation preference*** (Nitter, 1993). An example from the same author will be discussed in the following.

The same author reported from Merrell *et al.* (1979) who first pointed out that the inevitable differences in quality of crossbred generations can be used economically. As can be seen in Fig. 2, contrary to conventional rotational crossing in which there is only one flock in each crossbreeding year, in this system which can be a two-breed rotational crossing or criss-cross, there are 2 flocks rather than one. Also, a larger proportion of dams from the more prolific breed, than from the second breed which is superior e.g., in meat production, is kept in the flock. As a result, the proportion of slaughter animals having two thirds genes from the breed being superior in meat production is also higher. In sheep, the proportional number of ewes from the less fertile breed for this purpose can be 1/4, compared to that of ewes from the more prolific breed, being 3/4.

Also, unlike traditional rotational crossing systems, this system takes more advantages of complementarity of sire and dam due to the continuous expression of 76% heterosis in a larger proportion of offspring having more genes from the breed superior in meat production (breed B), every year.

This is because in traditional rotational systems, there is one flock rather than two, its dams being mated rotationally to the sires from different breeds, e.g., one year to breed A (more prolific), and the following year to breed B (more meat). In traditional rotational crossing systems, there will be the same proportion of heterosis (67%) expressed as that in the modified systems, but the proportion of offspring bearing B genes fluctuates dramatically (25%-75% in a 2-breed rotation, at equilibrium) from one year to another. This results in less performance level, in terms of the total body weight of lambs produced, reduced meat quality and price, and lack of the uniformity of the lamb crop quality for answering the market demands.

As mentioned above, in traditional rotational crossing systems the genotype of slaughter lambs changes significantly and thus, an irregular complementarity occurs i.e., the proportion of genes from breed A changes from 2/3 to 1/3 and then to 2/3 etc. But, in the modified crossing systems as presented in Fig. 2, we have 2 flocks with different sizes and different sire and dam breeds. A small flock helps make use of full complementarity in flock 1 which produces 83% of the total lambs

produced, but here, this system has the advantage of a stable proportion of sire and dam genes in the progeny every year which gives rise to a uniform production quality for flock 1 producing a large proportion of the crossbred production i.e. lamb.

The criss-cross rotation with generation preference, excerpted from Nitter (1993) is illustrated with modifications in presentation in Figure 2. It follows

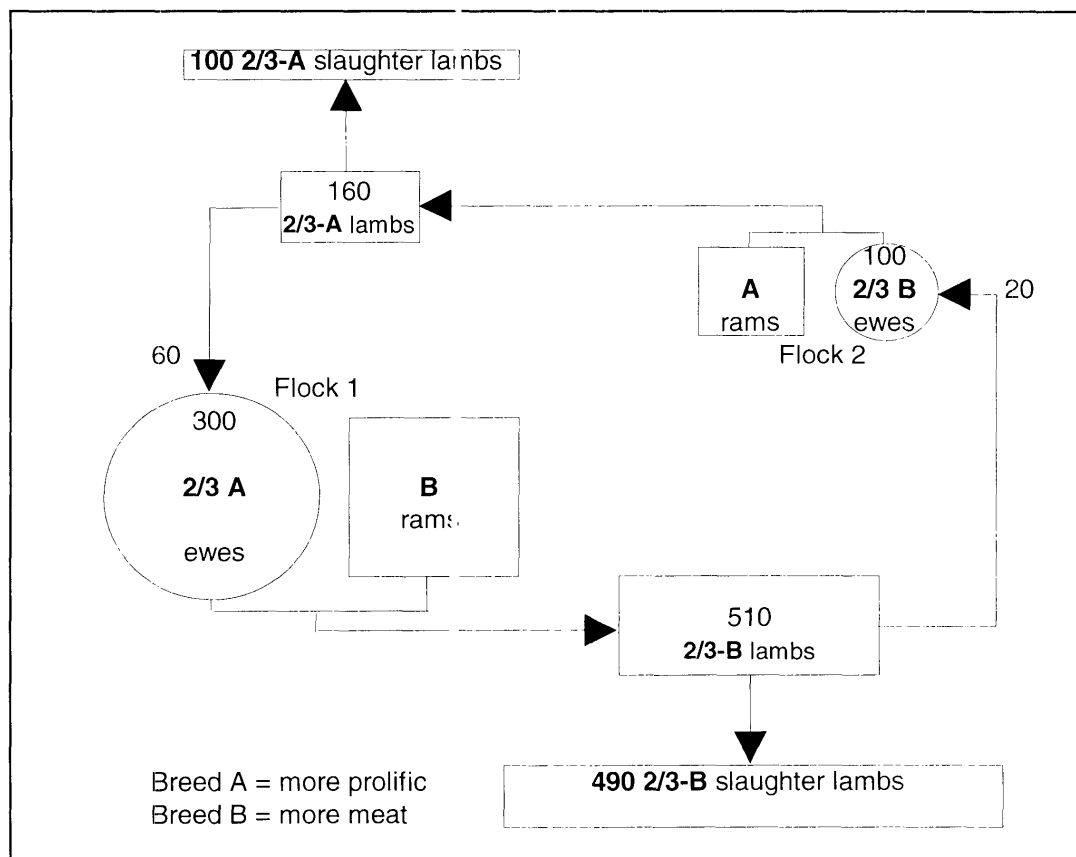


Figure 2. Criss-cross with generation preference.

that in this system two flocks exist in each year. Total number of the ewes in these two flocks is 400 heads with an average age of 5 years and thus with a ewe replacement rate of 20%. The ewes having $\frac{1}{3}$ of their genes from the more prolific breed A rear 1.6 lambs per year and those with $\frac{2}{3}$ -A gene ratio 1.7. After a number of years the system reaches an equilibrium at which stage by raising only 100 less prolific F_1 ewes in flock 2, the breeding system can be maintained. Meanwhile, 83% of the slaughter lambs in the main flock possess genes $\frac{2}{3}$ of which coming from

breed B being good in meat production. The same author remarked that proportion of the less fertile crossbred ewes i.e., $1/4 (=100 / (100 + 300))$ for maintaining the system can remarkably be reduced in highly prolific species, e.g., to one tenth in the pigs.

2) Terminal-rotation crossbreeding systems

Terminal-rotation crossbreeding systems are among the first modified systems. In these systems, a terminal sire is crossed on the females produced in a rotational crossing system which are no longer needed to produce replacement progeny (Gregory and Cundiff, 1980), and their offspring are all slaughtered. This can counterbalance the reduction in the breed effects and complementarity, where similar breeds are used in such a rotational crossing system in order to reduce the variability of merit over generations (Swan and Kinghorn, 1992). For better results, the previous authors proposed the use of a terminal sire on the older dams which are less likely to confront dystocia. As a consequence, there will be much breed differences in parental performance, much maternal heterosis and full direct heterosis (Hammond, 1994). Examples for terminal-rotation crossbreeding in beef cattle and in meat sheep will be given later in this Chapter, and in the DYNCSTBL.XLS model in Chapter 3, respectively. Also, as Nitter (1978) reported, Sidwell *et al.* (1964) discussed a proposed multi-bred sire rotation in the US for sheep, in which some of the paternal heterosis can be exploited.

3) Periodic rotational crossing systems

Periodic rotational crossbreeding systems are also modified system of rotations in which sire breeds are used unequally, to benefit from a higher percentage of better sire's genes. Nitter (1993) called these systems of rotational crossing *rotation with breed preference*. While in conventional rotations, in a complete cycle of n -breed, there is n generations, in each of which the sires are used only once, in periodic rotations sires can be used more than once. It results in more than n generations in a complete cycle of the crossing (Swan and Kinghorn, 1992). For instance, while in one cycle of a 3-breed conventional rotation sire breeds are used sequentially as A, B, C, in one cycle of a periodic rotation the sequence of sires may be A, B, B, A, A, C.

Conventional rotational crosses exploit maximum amount of heterosis possible in a rotational cross. However, they don't use maximum utilization of differences among the breeds in the cross (Bennett, 1987). Periodic

rotations can be found showing less variation in performance between generations compared with conventional rotations. In periodic rotations the differences between breeds result in improvement of progeny, but at the expense of the reduced heterosis (Nitter, 1993), and can lead to a higher performance compared with conventional rotational crosses where breed effects are sufficiently larger than heterosis. However, despite expressing less heterosis in periodic rotations, the exploitation of breed effects is possible. For instance, poorer breeds can be used less (Swan and Kinghorn, 1992).

Determinants and deterrents concerning uptake of crossbreeding systems

Several factors determine the appropriate crossing system for any particular situation. These factors are as follows (Dickerson, 1969; Swan and Kinghorn, 1992; Warwick and Legates, 1979):

- 1) Size of flock or herd.
- 2) The reproductive rate of species i.e., in some species of farm animals such as sheep, producing replacement females lessens the number of salable crossbred progeny.
- 3) The significance of heterosis and breed effects.
- 4) The balance between the amount of heterosis and breed of sire/dam complementarity in performance efficiency gained by the crossbreeding system.
- 5) The proportion of the total population which must be kept as straightbreds to provide the female replacements, or the availability of the female crossbreds to purchase for this reason.
- 6) The economic factors including the cost/return ratio of a specific crossing system in comparison with purebreeding programs.

Logistical and biological factors inhibiting uptake of crossbreeding are as follows (Swan and Kinghorn, 1992):

- 1) Extra management needed for crossbreeding systems compared with straightbreeding systems.

- 2) Importing crossbred animals incurs extra costs. Currently lack of pedigree for imported animals is a further obstacle in this regard.
- 3) Reproductive rate of species. For instance, in sheep and cattle the low reproductive rate of them requires derivation of a high proportion of straightbred animals (as replacements), giving rise to a declined crossbred production for sale.

A brief comparison of different crossing systems

Table 7 contrasts the major crossing systems described earlier in the text.

Table 7. Comparison of different crossing systems.

System of crossing	Heterosis	Ease	Replacements	Complementarity	Consistency	Accuracy
Up-grading	+ / 0	+	Yes	Case-related	+	+
2-breed crossing	+	+	No	High	+	+
3-breed crossing	++	-	No	Very high	++	+ / ?
4-breed crossing	+++	--	No	Highest	+++	+ / ?
2-breed rotation	+	-	Yes	Low	Varies	+
3-breed rotation	++	--	Yes	Very low	Highly varies	+
Synthetics	+	++	Yes	Ideal / nil, later	++	?
Synthetic - terminal	++	+	Yes	Ideal	+++	?

Crossbreeding is mainly applied to take advantage of heterosis and complementarity and/or to introduce new desirable genes to a particular population, or to substitute one breed for the other. This is called up-grading.

As there are different crossing systems, therefore, the amount of heterosis cannot properly be compared between different crosses of animals. In upgrading, maximum use of heterosis is in F_1 's (100%). In the subsequent back-crosses to the migrant breed, the amount of heterosis expression declines, so that in the 6th generation in an up-graded population, there would be almost no expression of heterosis. Among the crossing systems, 4-way crossings utilize maximum heterosis that can be obtained, due to expression of direct, maternal and paternal heterosis in the commercial progeny. Three-breed crossings also benefit highly from heterosis, but do not make use of paternal heterosis. Three- and four-breed crossings are widely being used in the poultry industry because poultry are highly prolific. Two-breed crosses benefit only from direct heterosis. Rotational crossing systems sacrifice some amount of heterosis and present less heterosis than specific two- or three-crossing systems with same number of breeds. With increasing the number of the breeds contributing to a crossing system, the heterosis expression increases, except for the established synthetics.

Synthetics make less use of heterosis in comparison with rotational or specific crosses with same variety of breeds involved in the crossing. To benefit from more heterosis, we can cross a terminal sire, breed or another synthetic breed, even a multi-bred sire over older dams from a rotational crossing or synthetic population.

The most pragmatic complementarity of sire and dam is attained by use of two specialized crossbred parental lines (double-two-way crossing). This technique has been practiced in the poultry industry for production of economic, fast growing, commercial chicks for a few decades, and is recently employed in the pig industry in some countries. The systems using such crossing systems utilize complementarity effects of sire and dam in both paternal and maternal lines. In three-breed crossing systems there is lesser use of complementarity as only one line or breed is used to produce sires and thus, the latter are not cross-breds. Therefore, no desirable blend of genes could be created in the paternal line. By use of synthetics, we can combine different attributes along with intense selection programs within a crossbred population. After a number of generations the ideal combination of different traits is achieved. But after this stage, no more complementarity of terminal-sire and dam occurs as only one breed is used. In the meantime, the complementary effects may decline after some generations, due to breakdown of favorable non-allelic gene combinations having additive effects. To further benefit from complementarity, the breeder can cross a reliable sire-breed of any desirable gene combination on synthetic dams continuously, or in some sequences using more than one sire-breed, provided these sires are from the breed-of-origin of the synthetic, unless they are from more superior exotic breeds.

In terms of ease of management, four-way crossings are the most complicated systems. They need excellent management, advanced facilities and a fairly good source of economic wealth. Ease of management depends on the number of breeds involved in the crossing and on the type of matings and provision of female replacements for crossing. With same number of breeds, synthetics have the least discomfort for the breeder, and in the second position there are traditional rotational crossing systems, as in these two kinds of crossing only one flock or herd exists and females are self-replacing, but sire rotation causes some marketing, feeding, and other problems. Upgrading has some complication in terms of performance recording and selection within the up-graded population and the degree of complication depends on the number of the up-graded generations.

In 4-way crossings, there is not a high consistency between complementarity and performance for favorable attributes in cross-bred populations before selection, as there is a great variation in the genetic material due to the relatively large number of the breeds being used. But, in the commercial products a good consistency between complementarity and consistency of performance exists as their parents are selected for favorable traits and combining abilities. Three-breed crosses and synthetic-terminals show a lower level of complementarity in comparison with 4-breed specific crosses, but they have a higher degree of consistency in progeny performance due to less variations in products resulting from a lower genotypic variance and from a lower possibility of segregation and recombination of non-allelic genes. Rotational crosses use a low to very low level of irregular complementarity due to the oscillation in crossbred product composition in consecutive generations. Therefore, the crossbred quality and even quantity varies notably between generations of crossing.

Accuracy of EBV's (Estimated Breeding Values) in rotational crosses could be relatively reliable as no replacement dams having dubious pedigrees are purchased from other breeding systems. If sires are not produced in the flock or herd, usually, quality sires or semen with enough reliability and sound pedigrees could easily be provided. Meanwhile, the possible recombination loss is less than that in synthetics, but it is higher in comparison with specific crosses. Therefore, EBV's of synthetic populations would not be as reliable as the other usual crosses. Three-way and especially four-way crossing systems are usually managed by big, private companies due to their special, complicated logistics, and usually extra care is taken in regard to performance recording, selection, and mating systems. However, the EBV's cannot always be deemed to be accurate enough, when crossbred animals are purchased for commercial purposes. Other details can be seen from Table 7.

1.4 - Importance of computer modeling

There is quite a wide range of breeds and strains of domestic animals being raised by humans for provision of various life essentials, all over the world. For a long period of time, researchers have worked out valuable information about the most important breeds and strains, including their prominent traits such as meat and wool production, etc. This information is valuable for a better utilization of within and between breed effects and of the genetic resources in the future. Also, trial crossing

experiments have been carried out throughout the world, and the preliminary information on crossing of different breeds has been obtained.

Additionally, within a complex of animal breeds, numerous ways of crossing exist, but only very few of them could be satisfactorily economical as the choice of breed and the flock structure can vary remarkably depending on the level of knowledge and meticulousness of the breeder. A scientific and economical animal breeding needs a precise decision making for mating of animals based on this information and other aspects of breeding. This cannot easily be achieved without employment of the computer. To determine the optimum structure of the population in crossbreeding enterprises which is directly associated with the management and economic aspects, simulation modeling of crossbreeding systems will have a high degree of importance. It helps the breeder make best use of animal resources with the highest profitability possible.

Systems analysis techniques enable us as to know how the genetic, management or environmental changes affect the system or how the system should be used for testing new hypothesis (Cartwright, 1979). Computer or mathematical modeling is a major tool of systems analysis by which our own mental image of the system is clearly exposed. Additionally, a more complete perspective of the related problems is offered for decision makers by giving numerical value for general statement of size, management and influence (Forrester, 1968). Also, by means of computer modeling, various combinations can be tested at relatively low cost in a short time (Bourdon and Brinks, 1987) and evaluation of short- and long-term tactical and strategic decisions for achieving desired production goals can be feasible (Blackburn and Cartwright, 1987).

Simulation modeling provides potential for understanding of the interface between breeding and production in a more detailed and mechanistic way (Harris and Newman, 1994) and should be more mechanistic for increasing the flexibility and effectiveness of production in a wide range of situations (Baldwin, 1976). Further, with simulation, design of breeding programs can be fulfilled while considering the economic value of the genetic changes. Multi-trait selection, simultaneous selection and crossbreeding and the system for disseminating genetic improvement seem appropriate for further study through simulation modeling. Another relevant use of simulation is in design of production systems for an efficient use of genetically improved livestock. As an example, in intensive production systems for poultry and swine, when performance potentials

change, the diets are often required to be changed. (Harris and Newman, 1994).

1.5 - Some examples of computer modeling

Over the past quarter century, many researchers have developed simulation models to study the effect of genetic improvement procedures on animal production systems in some species such as beef, sheep and swine. For instance, two series of studies in sheep are by Blackburn and Cartwright (1987 a, b, c) and Wang and Dickerson (1991 a, b, c). According to Harris and Newman (1994), the latter which involves the economic impact of fundamental biological traits on production systems of sheep, the tangent of slope of curves which presents the relationships concerned, could become a linear objective function. The results and possible application of this series of studies are as follows:

- a) "the measures of efficiency or combinations of genetic, management, and marketing variables can provide the relative economic weighting of traits needed to derive optimal criteria for genetic selection among and within breeds under defined industry production systems".
- b) "the estimates for relative economic importance of traits, apply to derivation of optimal criteria for genetic selection among breeds or crosses, or within-breeds used in rotation crossbreeding, but would differ for special terminal-sire or terminal breed roles."
- c) "these results should aid in development of optimum selection criteria for stocks used for pure or rotation crossbreeding or maternal parents of terminal crosses".

Similar studies in beef are by Wilton *et al.* (1974), Morris *et al.* (1976).

In terms of the reliability of the results obtained from simulation modeling, the question arises as to how accurate they can be. It seems that with enough meticulousness, a satisfactory accuracy can be obtained. Some researchers (Pomar and Harris, 1991; Blackburn and Cartwright, 1987; Pomar *et al.*, 1991) tested the results of their simulation modeling through investigating output of the models under actual specific conditions, and concluded that the models adequately simulated the animal flow and dynamic of the population; the response of the sheep in some production environments; and the growth and body composition of the young animals, respectively.

In the meantime, some researchers have developed different computer programs for optimization of populations for straightbreeding programs or for crossbreeding systems in sheep, beef and the pigs.

Barwick (1993) introduced a PC program for derivation of the economic weights for beef cattle called B-object. Its range of applications were developed to include some crossbred applications as well. It was intended as a mechanism to introduce formalized breeding objectives to the industry and to facilitate multi-trait selection.

Also, Nitter and Grasser (1993) developed a PC program called ZPLAN. It is described to be a deterministic multi-trait model for optimization of selection strategies in livestock breeding. The program calculates a number of criteria such as genetic gain for the breeding objective, the genetic gain for single traits, as well as profit for various breeding programs. The relevant parameters should be defined by the user. This is done by use of the gene-flow method and selection index procedure. In addition to other features of the program, it can also be applied to the populations used in crossbreeding systems.

A specific PC program for the design of crossbreeding systems called CS, was developed by Saviky (1993). This program evaluates the economic consequences for management decisions concerning mating plans with animals of up to 4 breeds of sheep and/or pigs. The model is static and deterministic and predicts the performances, the population structure, and the economic efficiency for an established population at equilibrium in terms of size and genetic composition, in absence of selection programs.

An example of a generalized optimum crossbreeding model is given in Figure 3. The source for reproducing this figure is Goddard (1994). The author describes a crossbreeding system in which the structure of the population is optimized by running a computer program. Depending on the input data, the computer model proposes either a simple terminal crossing, a rotational crossing, or a terminal-rotation crossing system. The figure presents an optimized terminal-rotation cross.

In this proposed crossing system, it is assumed that the gene proportions of the sires A and B in herds 1 and 2 have already reached an equilibrium after several years of crossing. Then, the cows in herd 1 will have $2/3$ of their genes from breed A being good in terms of meat production, and those in herd 2 will have $1/3$ of their genes from breed A and $2/3$ from breed B possessing good dam traits. Meanwhile, proportion of the genes

in the heifers is reverse so as $2/3$ of the heterosis is expressed. As the proportion of the steers and heifers with $2/3$ -A gene ratio being produced in herd 2 is higher than that in herd 1 therefore, some use of complementarity is made through preference of generation which was described earlier.

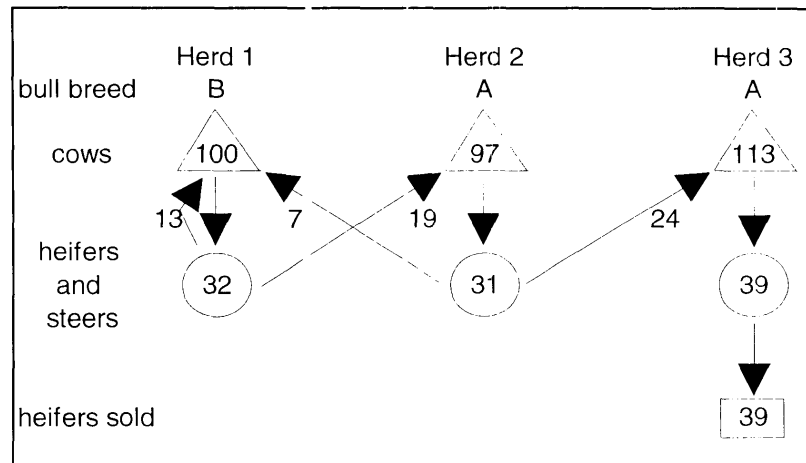


Figure 3. An example of a generalized crossbreeding model proposing an optimal terminal-rotation crossing system.