

KEYNOTE ARTICLES

HETEROISIS RETENTION AND INTER-BREED RECOMBINATION AMONG NON-ALLELIC GENES ASSOCIATED WITH CROSSBREEDING AND SYNTHESIS OF BREEDS

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ABSTRACT

Systematic crossbreeding and newly developed synthetic populations based on complementary breeds of exotic and/or indigenous origin, in conjunction with selection for specific objectives among economically important traits has consistently expedited rapid genetic improvement of production efficiency along with the income and profitability of the livestock and poultry enterprises. The breakdown of desirable combinations of segregating alleles inherited from many of the parental breeds during crossbreeding or the development of synthetic populations could lead to loss of desirable morphological characteristics and production performance. This may be attributed to the inter-breed recombination among non-allelic genes (epistasis) decreasing the proportion of retained heterosis, both direct and maternal. In addition to recombination loss, selection over subsequent generations increase the loss of within breed variability, decrease effective population size and hasten the rate of inbreeding. Research results on recombination loss in the parents and their offspring have often been conflicting. Precise estimates require large numbers of breeds and their crosses independent of environmental influence. The objective of the present study is to discuss crossbreeding strategies capable of retaining heterosis in the following generations while enhancing genetic merit of parents and their offspring.

Key words: *Sheep, Composite breed population, Additive and non-additive genetic components.*

INTRODUCTION

One should not be surprised to learn skilful breeders' privy to ancestral knowledge made use of crossbreeding long before the basic principles of quantitative genetics were elucidated and recommended by specialists and willingly accepted for commercial production. Research establishments worldwide have provided irrefutable evidence to suggest crossbred livestock and poultry obtained in a systematic manner grew rapidly, were more fecund and survived in greater proportion than their purebred contemporaries (**Gowen, 1952**). At the same time, animals and animal products derived from crossbred livestock and poultry have been widely accepted by consumers worldwide. Sheep producers' not only benefited from heterosis among complementary breed crosses but also profited from outstanding genetic merit of their parental breeds, leading to rapid and permanent improvement of reproduction, lean muscle growth, milk yield and composition, hardiness, and grease fleece weight and wool quality. Extensive literature on this subject has been published (**Rae, 1952; Winters, 1953, 1954; Terrill, 1958, 1974; Bichard, 1974; Land and Robinson, 1985; Fahmy, 1996a**).

Breeds are known to vary in average gene frequencies, allelic heterozygosity and non-allelic gene combinations which may have resulted from evolutionary forces, as well as in response to artificial selection for specific objectives, varying management, diet and environment, and most importantly the accumulation of random changes in gene frequencies over successive generations. According to **Dickerson (1969a)** productivity may be lost from random interbreed recombination of favourable joint effects among non-allelic genes, which were fixed in the parental breeds. This would influence the relative efficiencies of crossbreeding strategies employed to increase productivity. Nevertheless, greater initial heterozygosity of newly developed breeds unless lost through inbreeding in the early generations, should result in higher initial performance (**Sumption et al., 1961**). Many of the new breeds of sheep have been described in comprehensive studies (**Maijala and Terrill, 1991; Mason, 1980, 1996; Rasali et al., 2006**). However present methods employed for their development differ from the older principally in the intensity and the deliberate application of a greater store of knowledge on quantitative genetics (**Dickerson, 1969b; Lopez-Fanjul, 1974; Shrestha and Heaney, 2003, 2004**).

The concept of a composite population has become an integral part of breeding approach employed by the livestock and poultry industries for commercial production of breeding stock worldwide. This is regardless of the theoretically lower genetic potential for composite population performance versus that of a specific or rotational cross involving the same number of swine breeds (**Shrestha, 1973**). A simple procedure for developing a composite population based on equal proportions of three or more breeds consists of backcrossing offspring of a three-breed cross to the two-breed cross parents, followed by subsequent mating the crossbred offspring derived from the previous mating to males of the three-breed cross parent (**Lauprecht, 1961; Shrestha,**

KEYNOTE ARTICLES

005). The crossbred population is closed following the second generation of mating and subjected to random breeding, where every female has an equal chance of mating with every male. Concurrently in Germany, **Nitter and Fewson (1974)** proposed an interesting approach for the development of a synthetic dam line for meat production in sheep. Maintaining as large a segregating foundation population as possible with sufficient genetic variability to achieve recurrent genetic improvement of morphological characteristics and production performance from selection for optimal breeding objectives is always advantageous. Concurrently, the detrimental influence arising from increased inbreeding must be avoided at all costs.

Despite major achievements in the theory and application of quantitative genetic principles to the breeding of livestock and poultry, much of the effort practiced in the breeding of sheep has been haphazard, having failed to approach potential biological ceilings (**Wilson, 1968**). A realistic goal for the commercial production of meat sheep would be to have ewes reproduce first at 1-yr of age and later at 6-mo intervals along with increased prolificacy thereby doubling or even quadrupling existing levels of fecundity, reduction of lamb and ewe mortality, increasing milk yield, avoidance of extra costs associated with the production of unwanted fat in rapidly growing offspring often marketed at 45 kg around 100 days of age, improved fleece and wool quality, while making efficient use of readily available human and feed resources. In sheep, heterosis estimates derived as the average deviation in performance of reciprocal crosses from their respective purebred averages for a number of economically important traits demonstrate considerable potential for increasing productivity (**Nitter, 1978**). Estimates of recombination loss in the literature tend to vary considerably more compared to those for heterosis demonstrating the difficulty of obtaining precise estimates (**Young et al., 1986**), and often resulting in conflicting conclusions. The subject of the present review deals with crossbreeding strategies to maximize the genetic response to selection attributable to additive genetic, heterosis and recombination components inherited in the offspring are a consequence of genes transmitted directly from both parents, as well as through the environment provided by the maternal and paternal parents, and the maternal grand-parent of the maternal parent.

THEORETICAL EXPECTATION FOR GENETIC COMPONENTS OF INHERITANCE

The average effect in the purebred offspring of breeds 'A', 'B', 'C', 'D', etc, results from genes transmitted directly from their parents (g'_A, g'_B, g'_C, g'_D , etc); through the environment provided by their maternal ($g^M_A, g^M_B, g^M_C, g^M_D$, etc) and paternal ($g^P_A, g^P_B, g^P_C, g^P_D$, etc) parents, and the environment provided by the maternal grand-parent ($g^{M^M}_A, g^{M^M}_B, g^{M^M}_C, g^{M^M}_D$, etc) to the maternal parent (**Dickerson 1969a,b; 1973**). Similarly the average effect in the crossbred offspring resulting from genes transmitted directly from

parents of two or more breeds 'A', 'B', 'C', 'D', etc, will have their proportions vary according to the genetic composition in their offspring (g'_{AB} , g'_{AC} , g'_{AD} , g'_{BC} , etc); through the environment provided by their maternal (g^M_{AB} , g^M_{AC} , g^M_{AD} , g^M_{BC} , etc), and paternal parents (g^P_{AB} , g^P_{AC} , g^P_{AD} , g^P_{BC} , etc), and the environment provided by the maternal grand-parent to the maternal parent ($g^{M'}_{AB}$, $g^{M'}_{AC}$, $g^{M'}_{AD}$, $g^{M'}_{BC}$, etc). The expectation for the contribution of the male and female parents is based on their components as individuals, and those of the grand-parents are based on their components as parents. For simplicity the environment provided by the paternal grand-parents to the paternal parent as well as the maternal grand-sire to the maternal parent will not be considered in the expectations here.

Heterosis in the crossbred offspring results from an increase in average heterozygosity (dominance) along with any non-allelic interaction (epistasis) of the gametes of their respective parents, with proportions varying according to the genetic composition of the offspring (h'_{AB} , h'_{AC} , h'_{AD} , h'_{BC} , etc); through the environment provided by their maternal (h^M_{AB} , h^M_{AC} , h^M_{AD} , h^M_{BC} , etc), and paternal parents (h^P_{AB} , h^P_{AC} , h^P_{AD} , h^P_{BC} , etc), and the maternal grand-parent ($h^{M'}_{AB}$, $h^{M'}_{AC}$, $h^{M'}_{AD}$, $h^{M'}_{BC}$, etc) to the maternal parent. Despite evidence indicative of a non-linear relationship of dominance and recombination effects with percent heterozygosity (Wallace, 1958), expectations here are based on assumption of a linear relationship (Carmon et al., 1956). Again for simplicity, expectations resulting from the joint effects of individual components will not be considered. It should be noted that heterosis derived from linear contrasts of various breeds and their crossbred combinations is estimated at the level of the 'gametes', and is comprised of both intra- and inter-allelic interactions. Recombination of segregating alleles between chromosomes of the parents results from non-allelic gene interaction effects in the crossbred offspring relative to those of their purebred and crossbred parents (r'_{AB} , r'_{AC} , r'_{AD} , r'_{BC} , etc); through the environment provided by their maternal (r^M_{AB} , r^M_{AC} , r^M_{AD} , r^M_{BC} , etc) and paternal parents (r^P_{AB} , r^P_{AC} , r^P_{AD} , r^P_{BC} , etc), and the maternal grand-parent ($r^{M'}_{AB}$, $r^{M'}_{AC}$, $r^{M'}_{AD}$, $r^{M'}_{BC}$, etc) to the maternal parent. All individual components are defined as mean deviation in the performance of the offspring from the average of the parental pure breeds. Alternative approaches based on dominance and epistatic effects in the performance of the offspring and their parents at the level of the 'gamete' and 'genotype' have been discussed extensively in the literature (Gowen, 1952; Hayman and Mather, 1955; Hayman, 1958; Jinks and Jones, 1958; Kinghorn, 1980; Hill, 1982). Despite differences in their notation, parameter estimates for performance of the offspring and their parents at the level of the 'gamete' and 'genotype' were found to have comparable expectations resulting in similar conclusions (Koch et al., 1985). This is because the expectations among different sets of parameters based on heterosis and recombination components correspond to those derived from dominance and epistatic effects.

KEYNOTE ARTICLES

Theoretical expectations showing proportions for additive genetic (g), heterosis (h) and recombination (r) components in the offspring have been presented for the following: Purebred and two-breed crosses (F_1 , F_2 and F_3) in Table 1 and Figure 1; Back-crosses (BC_1 , BC_2 and BC_3) in Table 2 and Figure 2; specific three- and four-breed crosses in Table 3 and Figure 3; two-, three- and four-breed Rotational crosses in Table 4 and Figure 4; and two-, three- and four breed Synthetic populations (with equal proportions of breeds) in Table 5 and Figure 5. Expectations in the offspring have also been presented for Terminal crosses derived from mating a purebred sire with the following: three- and four-breed Backcrosses (BC_1) in Table 6 and Figure 6; two-, three- and four-breed Rotational crosses in Table 7 and Figure 6; and two-, three- and four breed Synthetic populations (with equal proportions of breeds) in Table 8 and Figure 6. This approach for defining theoretical expectation can be extended to Synthetic populations with unequal proportion of parental breeds.

PARAMETER ESTIMATION

There is agreement among researchers that environment which includes location, season, age of dam, sex, type of birth and rearing and body weight have important influences on morphological characteristics and production performance in sheep. Genotype x environment interaction is another source of variation that has been reported to influence economically important performance traits when large differences occur among breeds and/or environments. Properly designed studies should facilitate the estimation of genetic effects for performance independent of the environment, thus minimizing the contribution of genotype x environment interaction. If there are large differences in the performance of each sex, it has been suggested that analyses should be carried out separately by sex.

Inbreeding which arises from the mating of parents that are more closely related to each other than the average of the population has an important influence in the genotype frequency of the offspring. This is because related parents are more likely to transmit the same genes to their offspring than unrelated parents. In practice, a simple procedure for calculating inbreeding coefficients proposed by **Emik and Terrill (1949)** and based on co-ancestry, has been used widely. Also discussed extensively in the literature (**Gowen, 1952**) is the detrimental influence of inbreeding which reduces the overall vigour of the offspring and their parents, and has greater influence in traits associated with fitness, such as conception, fertility, prolificacy and survival. The influence of inbreeding on genetic components can be accounted for in the theoretical expectations but is cumbersome and complex. Therefore it will not be considered here. Most importantly, estimates of theoretical expectations for genetic components of inheritance are subject to sampling variation. In order to obtain precise estimates while avoiding any undesirable influence on production performance that could result from an increase in rate of inbreeding, the effective number of male and female parents in the

population needs to be adequate (Shrestha et al., 2010). Furthermore, studies replicated over time and location will produce results that have a wider application.

The individual genetic components partitioned into additive genetic, heterotic and recombination effects as shown in Tables 1-8 are based on general procedures proposed by Dickerson (1969a,b, 1973; FAO, 1993). These components have specific application in assessing the relative merit of various crossbreeding strategies, and are presented as deviation from an average of their respective maternal and paternal parental breeds in the following:

F₁, F₂, and F₃:

$$(AxB) - \bar{A} - \bar{B} = h_{AB}^M + \frac{1}{2}(g_B^M - g_A^M) + \frac{1}{2}(g_A^P - g_B^P) + \frac{1}{2}(g_B^{M'} - g_A^{M'})$$

$$(AxB)^2 - \bar{A} - \bar{B} = \frac{1}{2}h_{AB}^I + r_{AB}^I + h_{AB}^M + h_{AB}^P + \frac{1}{2}(g_B^{M'} - g_A^{M'})$$

$$(AxB)^3 - \bar{A} - \bar{B} = \frac{1}{2}h_{AB}^I + r_{AB}^I + \frac{1}{2}h_{AB}^M + r_{AB}^M + \frac{1}{2}h_{AB}^P + r_{AB}^P + h_{AB}^{M'}$$

BC₁, BC₂ and BC₃:

$$Ax(AxB) - \bar{A} - \bar{B} = \frac{1}{4}(g_A^I - g_B^I) + \frac{1}{2}h_{AB}^I + \frac{1}{2}r_{AB}^I + h_{AB}^M + \frac{1}{2}(g_A^P - g_B^P) + \frac{1}{2}(g_B^{M'} - g_A^{M'})$$

$$Ax\{Ax(AxB)\} - \bar{A} - \bar{B} = \frac{3}{8}(g_A^I - g_B^I) + \frac{1}{4}h_{AB}^I + \frac{1}{4}r_{AB}^I + \frac{1}{4}(g_A^M - g_B^M) + \frac{1}{2}h_{AB}^M + \frac{1}{2}r_{AB}^M + \frac{1}{2}(g_A^P - g_B^P) + h_{AB}^{M'}$$

$$Ax\{Ax\{Ax(AxB)\}\} - \bar{A} - \bar{B} = \frac{7}{16}(g_A^I - g_B^I) + \frac{1}{8}h_{AB}^I + \frac{1}{8}r_{AB}^I + \frac{3}{8}(g_A^M - g_B^M) + \frac{1}{4}h_{AB}^M + \frac{1}{4}r_{AB}^M + \frac{1}{2}(g_A^P - g_B^P) + \frac{1}{4}(g_A^{M'} - g_B^{M'}) + \frac{1}{2}h_{AB}^{M'} + \frac{1}{2}r_{AB}^{M'}$$

Specific three- and four-breed cross:

$$Ax(BxD) - \bar{A} - \bar{B} - \bar{D} = \frac{1}{6}g_A^I - \frac{1}{6}(g_B^I + g_D^I) + \frac{1}{2}(h_{AB}^I + h_{AD}^I) + \frac{1}{2}r_{BD}^I - \frac{1}{3}g_A^M + \frac{1}{6}(g_B^M + g_D^M) + h_{BD}^M + \frac{2}{3}g_A^P - \frac{1}{3}(g_B^P + g_D^P) + \frac{2}{3}g_D^{M'} - \frac{1}{3}(g_A^{M'} + g_B^{M'})$$

$$(AxB)x(CxD) - \bar{A} - \bar{B} - \bar{C} - \bar{D} = \frac{1}{4}(h_{AC}^I + h_{AD}^I + h_{BC}^I + h_{BD}^I) + \frac{1}{2}r_{CD}^I + \frac{1}{4}(g_C^M + g_D^M) - \frac{1}{4}(g_A^M + g_B^M) + h_{CD}^M + \frac{1}{4}(g_A^P + g_B^P) - \frac{1}{4}(g_C^P + g_D^P) + h_{AB}^P + \frac{2}{4}g_D^{M'} - \frac{1}{4}(g_A^{M'} + g_B^{M'} + g_C^{M'})$$

Two-, Three- and Four-breed Rotational cross (each type of cross with equal proportion of the parental breeds):

$$(A::B) - \bar{A} - \bar{B} = \frac{2}{3}h_{AB}^I + \frac{1}{3}r_{AB}^I + \frac{2}{3}h_{AB}^M + \frac{1}{3}r_{AB}^M + \frac{2}{3}h_{AB}^{M'} + \frac{1}{2}r_{AB}^{M'}$$

$$(A::B::C) - \bar{A} - \bar{B} - \bar{C} = \frac{6}{21}(h_{AB}^I + h_{AC}^I + h_{BC}^I) + \frac{3}{21}(r_{AB}^I + r_{AC}^I + r_{BC}^I) + \frac{6}{21}(h_{AB}^M + h_{AC}^M + h_{BC}^M) + \frac{3}{21}(r_{AB}^M + r_{AC}^M + r_{BC}^M) + \frac{6}{21}(h_{AB}^{M'} + h_{AC}^{M'} + h_{BC}^{M'}) + \frac{3}{21}(r_{AB}^{M'} + r_{AC}^{M'} + r_{BC}^{M'})$$

$$(A::B::C::D) - \bar{A} - \bar{B} - \bar{C} - \bar{D} = \frac{14}{90}(h_{AB}^I + h_{AC}^I + h_{AD}^I + h_{BC}^I + h_{BD}^I + h_{CD}^I) + \frac{7}{90}(r_{AB}^I + r_{AC}^I + r_{AD}^I + r_{BC}^I + r_{BD}^I + r_{CD}^I) + \frac{14}{90}(h_{AB}^M + h_{AC}^M + h_{AD}^M + h_{BC}^M + h_{BD}^M + h_{CD}^M) + \frac{7}{90}(r_{AB}^M + r_{AC}^M + r_{AD}^M + r_{BC}^M + r_{BD}^M + r_{CD}^M) + \frac{14}{90}(h_{AB}^{M'} + h_{AC}^{M'} + h_{AD}^{M'} + h_{BC}^{M'} + h_{BD}^{M'} + h_{CD}^{M'}) + \frac{7}{90}(r_{AB}^{M'} + r_{AC}^{M'} + r_{AD}^{M'} + r_{BC}^{M'} + r_{BD}^{M'} + r_{CD}^{M'})$$

Two-, Three- and Four-breed Synthetic populations (each type of cross with equal proportion of the parental breeds):

$$(A \approx B) - \bar{A} - \bar{B} = \frac{1}{2} h_{AB}^i + \frac{1}{2} r_{AB}^i + \frac{1}{2} h_{AB}^M + \frac{1}{2} r_{AB}^M + \frac{1}{2} h_{AB}^P + \frac{1}{2} r_{AB}^P + \frac{1}{2} h_{AB}^{M'} + \frac{1}{2} r_{AB}^{M'}$$

$$(A \approx B \approx C) - \bar{A} - \bar{B} - \bar{C} = \frac{2}{9} (h_{AB}^i + h_{AC}^i + h_{BC}^i) + \frac{2}{9} (r_{AB}^i + r_{AC}^i + r_{BC}^i) + \frac{2}{9} (h_{AB}^M + h_{AC}^M + h_{BC}^M) + \frac{2}{9} (r_{AB}^M + r_{AC}^M + r_{BC}^M) + \frac{2}{9} (h_{AB}^P + h_{AC}^P + h_{BC}^P) + \frac{2}{9} (r_{AB}^P + r_{AC}^P + r_{BC}^P) + \frac{2}{9} (h_{AB}^{M'} + h_{AC}^{M'} + h_{BC}^{M'}) + \frac{2}{9} (r_{AB}^{M'} + r_{AC}^{M'} + r_{BC}^{M'})$$

$$(A \approx B \approx C \approx D) - \bar{A} - \bar{B} - \bar{C} - \bar{D} = \frac{3}{24} (h_{AB}^i + h_{AC}^i + h_{AD}^i + h_{BC}^i + h_{BD}^i + h_{CD}^i) + \frac{3}{24} (r_{AB}^i + r_{AC}^i + r_{AD}^i + r_{BC}^i + r_{BD}^i + r_{CD}^i) + \frac{3}{24} (h_{AB}^M + h_{AC}^M + h_{AD}^M + h_{BC}^M + h_{BD}^M + h_{CD}^M) + \frac{3}{24} (r_{AB}^M + r_{AC}^M + r_{AD}^M + r_{BC}^M + r_{BD}^M + r_{CD}^M) + \frac{3}{24} (h_{AB}^P + h_{AC}^P + h_{AD}^P + h_{BC}^P + h_{BD}^P + h_{CD}^P) + \frac{3}{24} (r_{AB}^P + r_{AC}^P + r_{AD}^P + r_{BC}^P + r_{BD}^P + r_{CD}^P) + \frac{3}{24} (h_{AB}^{M'} + h_{AC}^{M'} + h_{AD}^{M'} + h_{BC}^{M'} + h_{BD}^{M'} + h_{CD}^{M'}) + \frac{3}{24} (r_{AB}^{M'} + r_{AC}^{M'} + r_{AD}^{M'} + r_{BC}^{M'} + r_{BD}^{M'} + r_{CD}^{M'})$$

Terminal cross with three- and four-breed BC₁:

$$Cx(Ax(AxB)) - \bar{A} - \bar{B} - \bar{C} = \frac{1}{6} g_C^i + \frac{1}{24} g_A^i - \frac{5}{24} g_B^i + \frac{3}{4} h_{CA}^i + \frac{1}{4} h_{CB}^i + \frac{1}{4} r_{AB}^i + \frac{5}{12} g_A^M - \frac{1}{12} g_B^M - \frac{1}{3} g_C^M + \frac{1}{2} h_{AB}^M + \frac{1}{2} r_{AB}^M + \frac{2}{3} g_C^P - \frac{1}{3} g_A^P - \frac{1}{3} g_B^P + \frac{1}{6} (g_A^{M'} + g_B^{M'}) - \frac{1}{3} g_C^{M'} + h_{AB}^{M'}$$

$$Dx[Cx(Ax(AxB))] - \bar{A} - \bar{B} - \bar{C} - \bar{D} = \frac{1}{4} g_D^i - \frac{1}{16} g_A^i - \frac{3}{16} g_B^i + \frac{1}{2} h_{DC}^i + \frac{3}{8} h_{DA}^i + \frac{1}{8} h_{DB}^i + \frac{3}{8} r_{CA}^i + \frac{1}{8} r_{CB}^i + \frac{1}{4} g_C^M + \frac{1}{4} g_A^M - \frac{1}{8} g_B^M - \frac{1}{4} g_D^M + \frac{3}{4} h_{CA}^M + \frac{1}{4} h_{CB}^M + \frac{1}{4} r_{AB}^M + \frac{3}{4} g_D^P - \frac{1}{4} (g_A^P + g_B^P + g_C^P) + \frac{1}{2} g_A^{M'} - \frac{1}{4} (g_C^{M'} + g_D^{M'}) + \frac{1}{2} h_{AB}^{M'} + \frac{1}{2} r_{AB}^{M'}$$

Terminal cross with two-, three- and four-breed Rotational cross (each type of cross with equal proportion of the parental breeds):

$$Cx(A::B) - \bar{A} - \bar{B} - \bar{C} = \frac{1}{6} g_C^i - \frac{1}{12} (g_A^i + g_B^i) + \frac{1}{2} (h_{CA}^i + h_{CB}^i) + \frac{1}{2} r_{AB}^i + \frac{1}{6} (g_A^M + g_B^M) - \frac{1}{3} g_C^M + \frac{2}{3} h_{AB}^M + \frac{1}{3} r_{AB}^M + \frac{2}{3} g_C^P - \frac{1}{3} (g_A^P + g_B^P) - \frac{1}{3} g_C^{M'} + \frac{1}{6} (g_A^{M'} + g_B^{M'}) + \frac{2}{3} h_{AB}^{M'} + \frac{1}{3} r_{AB}^{M'}$$

$$Cx(A::B::D) - \bar{A} - \bar{B} - \bar{C} - \bar{D} = \frac{1}{4} g_C^i - \frac{1}{12} (g_A^i + g_B^i + g_D^i) + \frac{1}{3} (h_{CA}^i + h_{CB}^i + h_{CD}^i) + \frac{5}{63} (r_{AB}^i + r_{AD}^i + r_{BD}^i) - \frac{1}{4} g_C^M + \frac{1}{12} (g_A^M + g_B^M + g_D^M) + \frac{5}{21} (h_{AB}^M + h_{AD}^M + h_{BD}^M) + \frac{3}{21} (r_{AB}^M + r_{AD}^M + r_{BD}^M) + \frac{1}{4} g_C^P - \frac{1}{4} (g_A^P + g_B^P + g_D^P) - \frac{1}{4} g_C^{M'} + \frac{1}{12} (g_A^{M'} + g_B^{M'} + g_D^{M'}) + \frac{5}{21} (h_{AB}^{M'} + h_{AD}^{M'} + h_{BD}^{M'}) + \frac{3}{21} (r_{AB}^{M'} + r_{AD}^{M'} + r_{BD}^{M'})$$

$$Zx(A::B::C::D) - \bar{A} - \bar{B} - \bar{C} - \bar{D} - \bar{Z} = \frac{3}{10} g_Z^i + \frac{1}{20} (g_A^i + g_B^i + g_C^i + g_D^i) + \frac{1}{4} (h_{ZA}^i + h_{ZB}^i + h_{ZC}^i + h_{ZD}^i) + \frac{14}{270} (r_{AB}^i + r_{AC}^i + r_{AD}^i + r_{BC}^i + r_{BD}^i + r_{CD}^i) - \frac{1}{5} g_Z^M + \frac{1}{20} (g_A^M + g_B^M + g_C^M + g_D^M) + \frac{14}{90} (h_{AB}^M + h_{AC}^M + h_{AD}^M + h_{BC}^M + h_{BD}^M + h_{CD}^M) + \frac{7}{90} (r_{AB}^M + r_{AC}^M + r_{AD}^M + r_{BC}^M + r_{BD}^M + r_{CD}^M) + \frac{4}{5} g_Z^P - \frac{1}{5} (g_A^P + g_B^P + g_C^P + g_D^P) - \frac{1}{5} g_Z^{M'} + \frac{1}{20} (g_A^{M'} + g_B^{M'} + g_C^{M'} + g_D^{M'}) + \frac{14}{90} (h_{AB}^{M'} + h_{AC}^{M'} + h_{AD}^{M'} + h_{BC}^{M'} + h_{BD}^{M'} + h_{CD}^{M'}) + \frac{7}{90} (r_{AB}^{M'} + r_{AC}^{M'} + r_{AD}^{M'} + r_{BC}^{M'} + r_{BD}^{M'} + r_{CD}^{M'})$$

Terminal cross with two-, three- and four-breed Synthetic populations (each type of cross with equal proportion of the parental breeds):

$$Cx(A \approx B) - \bar{A} - \bar{B} - \bar{C} = \frac{1}{6} g_C^i - \frac{1}{6} (g_A^i + g_B^i) + \frac{1}{2} (h_{CA}^i + h_{CB}^i) + \frac{1}{2} r_{AB}^i + \frac{1}{6} (g_A^M + g_B^M) - \frac{1}{3} g_C^M + \frac{1}{2} h_{AB}^M + \frac{1}{2} r_{AB}^M + \frac{2}{3} g_C^P - \frac{1}{3} (g_A^P + g_B^P) - \frac{1}{3} g_C^{M'} + \frac{1}{6} (g_A^{M'} + g_B^{M'}) + \frac{1}{2} h_{AB}^{M'} + \frac{1}{2} r_{AB}^{M'}$$

$$Cx(A \approx B \approx D) - \bar{A} - \bar{B} - \bar{C} - \bar{D} = \frac{1}{4} g_C^i - \frac{1}{12} (g_A^i + g_B^i + g_D^i) + \frac{1}{3} (h_{CA}^i + h_{CB}^i + h_{CD}^i) + \frac{2}{9} (r_{AB}^i + r_{CD}^i + r_{BD}^i) -$$

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$$\frac{1}{4} g_C^M + \frac{1}{12} (g_A^M + g_B^M + g_D^M) + \frac{2}{9} (h_{AB}^M + h_{AD}^M + h_{BD}^M) + \frac{2}{9} (r_{AB}^M + r_{AD}^M + r_{BD}^M) + \frac{1}{4} g_C^P - \frac{1}{4} (g_A^P + g_B^P + g_D^P) - \frac{1}{4} g_C^M + \frac{1}{12} (g_A^M + g_B^M + g_D^M) + \frac{2}{9} (h_{AB}^M + h_{AD}^M + h_{BD}^M) + \frac{2}{9} (r_{AB}^M + r_{AD}^M + r_{BD}^M)$$

$$Zx(A \approx B \approx C \approx D) - \bar{A} - \bar{B} - \bar{C} - \bar{D} - \bar{Z} = \frac{3}{10} g_Z^I + \frac{1}{20} (g_A^I + g_B^I + g_C^I + g_D^I) + \frac{1}{4} (h_{ZA}^I + h_{ZB}^I + h_{ZC}^I + h_{ZD}^I) + \frac{1}{24} (r_{AB}^I + r_{AC}^I + r_{AD}^I + r_{BC}^I + r_{BD}^I + r_{CD}^I) - \frac{1}{3} g_Z^M + \frac{1}{20} (g_A^M + g_B^M + g_C^M + g_D^M) + \frac{3}{24} (h_{AB}^M + h_{AC}^M + h_{AD}^M + h_{BC}^M + r_{BD}^M + h_{CD}^M) + \frac{3}{24} (r_{AB}^M + r_{AC}^M + r_{AD}^M + r_{BC}^M + r_{BD}^M + r_{CD}^M) + \frac{4}{5} g_Z^P - \frac{1}{3} (g_A^P + g_B^P + g_C^P + g_D^P) - \frac{1}{3} g_Z^M + \frac{1}{20} (g_A^M + g_B^M + g_C^M + g_D^M) + \frac{3}{24} (h_{AB}^M + h_{AC}^M + h_{AD}^M + h_{BC}^M + h_{BD}^M + h_{CD}^M) + \frac{3}{24} (r_{AB}^M + r_{AC}^M + r_{AD}^M + r_{BC}^M + r_{BD}^M + r_{CD}^M)$$

The influence of heterosis on morphological characteristics and production performance may vary according to the inherent ability of breeds involved in crossing and the environment where the offspring raised. Furthermore, if heterosis in the economically important performance traits arises from epistasis, the role of specific gene combinations associated with multiple loci of the parental breeds need to be considered. **Nitter (1978)** in a comprehensive study of sheep breeds for meat production summarized the mean individual heterosis estimates (%), for lamb weights at birth and weaning, and pre- and post-weaning growth rates were 3.2, 5, 5.3, and 6.6, respectively; for yearling or adult body weights was 5.2; for fertility, prolificacy, lamb survival (lambs weaned of live lambs born, %), and fecundity were 2.6, 2.8, 9.8, and 15.2, respectively; and for total lamb weight per ewe exposed was 17.8. Concurrent estimates of mean maternal heterosis (%), for lamb weights at birth and weaning were 5.1, and 6.3, respectively; for ewe weight, and fleece weight were 5, and 13.4, respectively; for fertility, prolificacy, survival rate, and fecundity were 8.7, 3.2, 2.7, and 14.7, respectively; and total lamb weight per ewe exposed was 18. Following an extensive review of literature on heterosis in sheep, estimates and percentage of heterosis (individual, maternal, and paternal) for lamb weights at birth and weaning, pre- and post-weaning growth rates, yearling weight, fertility, prolificacy, lamb survival, fecundity, grease fleece weight, wool grade and total lamb weight weaned and marketed per ewe lambing (exposed) have been presented in Table 9. In Australia, **Ch'ang and Evans (1986)** evaluated the Dorset, Merino and Corriedale breeds and their crosses for paternal heterosis. The authors reported that estimates for all traits assessed except weaning weight, were favourable and in the desired direction. In general, published estimates for maternal and paternal heterosis lack the necessary precision because the majority of studies were based on small number of animals within purebreds and their crosses. Furthermore, large numbers of these studies were based on imported breeds and their crosses, with offspring grown in an environment which was nothing like their habitat, leading to concerns over the possibility of genotype x environment interaction effect on performance. Nevertheless these estimates from various studies worldwide have important significance for sheep breeding.

KEYNOTE ARTICLES

PREDICTION OF PERFORMANCE

An important issue in animal breeding is the choice of appropriate crossbreeding strategies such as systematic crossbreeding and synthetic populations to achieve potential genetic merit in the offspring and their parents and to identify the optimum cross that could approach maximum production efficiency. The difficult task of predicting performance of crossbred offspring lies in the number of possible combinations that need to be evaluated when multiple breeds are involved. Performance testing of two- and three-breed crosses alone neglecting reciprocals, can be a formidable task, and for a large number of breeds it could soon become impossible. A simple procedure has been proposed for prediction of performance of crossbred combinations of two or more breeds based on the average performance of parental breeds, raised under similar environment and management conditions as that of their crossbred offspring.

Carmon (1960) proposed a procedure to predict the performance of specific three breed cross [AxBxC] from the average performance of two-breed crosses i.e. (AxB) and (AxC), where A, B and C are parental breeds, with the exception of the cross (BxC), that was used to produce the crossbred female parent. Similarly, the performance of a four-breed cross [(AxB)x(CxD)] may be predicted from the average of two-breed crosses i.e. (AxC), (AxD), (BxC) and (BxD), where A, B, C and D are parental breeds. The crosses (AxB) and (CxD) that were used to produce the crossbred female parent are not included. In poultry, the above procedures for predicting performance of multiple crosses were found to be reliable for only a few traits (**Hill and Nordskog, 1958**). Prediction of performance among economic traits of multiple breed crosses will vary with the nature of genetic variation in those traits regardless of whether the two-breed crosses are raised under similar environment and management conditions.

In order to predict the performance of the Rotational cross and Synthetic population it is important to adjust for any reduction in heterozygosity as shown in their expectations. **Carmon et al. (1956)** also proposed a procedure to predict performance of rotational cross offspring (R_x) involving two or more (x) breeds from the difference in performance between average of all the single crosses derived from the purebred parental breeds included in the rotational cross (SC_x) and SC_x as a deviation from the average of the parental breeds (\overline{PB}_x) adjusted to account for reduction in heterozygosity in the rotational cross i.e. $R_x = SC_x - \frac{SC_x - \overline{PB}_x}{2^x - 1}$. In theory the reduction in heterozygosity

for rotational cross involving two-, three-, four- or more breeds is expected to be approximately $1/3^{\text{rd}}$, $1/7^{\text{th}}$, $1/15^{\text{th}}$, or more, respectively. Also, as the number of breeds in the rotational cross increases, the performance of the crosses is likely to approach the average performance of all single crosses derived from the same purebred parental breeds. The disadvantage with rotational crossing arises from the recurring use of

purebred sires to produce offspring in each generation, failing to benefit from breed difference in maternal versus individual performance. For the purpose of prediction of performance in the rotational cross, the following aspects have been ignored: the theoretical possibility of any change in performance arising from the re-arrangement of genetic combinations among the chromosomes of the crossbred parent, and further loss in maternal and individual performance from inter-breed recombination in gametes of the offspring resulting from their respective dam and maternal grand-dam.

The performance of the composite population (CP_x) involving two or more (x) breeds may be predicted from the difference in performance between the average of all the single crosses of the parental breeds included in the composite population (SC_x) and SC_x as a deviation from the average of the parental breeds (\overline{PB}_x) adjusted to take into account for the reduction in heterozygosity in the composite population i.e.

$$CP_x = SC_x - [(SC_x - \overline{PB}_x)(1 - \frac{x-1}{x})]$$

In theory the reduction in heterozygosity in the

composite population composed of two-, three-, four- or more breeds is expected to be approximately 1/2rd, 1/3rd, 1/4th or more, respectively. This is because a single population is not capable of exploiting breed difference in maternal versus individual performance. Nevertheless the loss in heterosis over successive generations of *inter se* breeding can be minimized if the initial unfavourable effects on performance due to rearrangement of genetic combinations are negligible.

The general approach used to arrive at predictions described above may be extended to terminal sire crosses of backcross, rotational cross and composite populations described in Tables 6-8 (Figure 6). It is possible to predict the performance of the terminal sire cross from the average performance of all possible single crosses between the terminal sire and the purebred parental breeds of the crossbred ewe. For example, the performance of the three breed terminal cross with backcross i.e. C x [A(AxB)] may be predicted from the average performance of two-breed crosses i.e. (CxA) and (CxB), where A, B and C are parental breeds, with the exception of the cross (AxB), that produced the crossbred female parent. Adjustments need to be made in order to account for the lower performance arising from theoretical reduction in heterozygosity in the crossbred ewe which would vary with the number of parental breeds assembled in accordance with the systematic crossbreeding strategy e.g. back-cross, rotational cross and composite populations.

HETEROSIS RETENTION AND RECOMBINATION LOSS

Breeds, populations and landraces selected for performance with no bearing on economic prospects under prevailing market conditions along with random changes in gene frequencies may have contributed to fixation of undesirable interbreed recombination among non-allelic genes. Only heterosis retained from desirable

KEYNOTE ARTICLES

combinations of interbreed recombination among non-allelic genes established in specific parental breeds is of interest and may be utilized effectively in assembling prospective breeds. When heterosis results from epistatic combinations fixed in their respective purebred parental breeds, especially with multiple loci, performance based on F_1 crosses may not be reliable for predicting heterosis retention in multiple breed crosses and in advanced generations of the newly developed composite breeds. Some of the desirable gene combinations associated with loss of production performance as a result of natural selection could possibly be harnessed with crossbreeding. Following an extensive review of literature in sheep, estimates of recombination loss based on difference between generations F_1 to F_2 , differences between composite population and the average of their respective purebred parental breeds, and heterosis retention for lamb weights at birth and weaning, pre- and post-weaning growth rates, yearling weight, fertility, prolificacy, lamb survival, fecundity, grease fleece weight, wool grade and total lamb weight weaned and marketed per ewe lambing (exposed) have been presented in Table 10.

The Romnelet breed developed in Canada from the Romney and Rambouillet breeds, declined in performance from generations F_1 to F_2 for lamb weights at birth, weaning and 18-mo of age and yearling clean fleece weight. In the subsequent generations, following estimates i.e. ($F_2 - F_3$), ($F_3 - F_4$), ($F_4 - F_5$), ($F_5 - F_6$), and ($F_6 - F_7$) were small and inconsistent (Peters et al., 1961). Crossbreeding studies involving the Border Leicester and Merino breeds in Australia revealed performance from F_1 to F_2 generation, resulted in significantly heavier greasy and clean fleece weight though only slightly greater face cover scores, whereas the decline was large and significant for fertility, prolificacy and lamb survival to weaning (Pattie and Smith, 1964). At the same time, 18-mo yearling weight, mutton score, fleece and breech score, yield and staple length, crimps per inch, fiber diameter, follicle density, ratio of primary to total follicles, and wool colour and character showed no change.

Further evidence of decline in performance from generations F_1 to F_2 was reported in New Zealand following the evaluation of the Border Leicester and Romney breeds and their crosses for birth weight, yearling weight, fertility, prolificacy, fecundity and lamb survival, with the exception for weaning weight and grease fleece weight (Hight and Jury, 1970a,b, 1971). In the subsequent generations leading up to generation F_4 , a small decline in performance was noted. Despite evidence signifying decline in performance from generations F_1 to F_2 and possibly in the subsequent generations, it is difficult to establish if inter-breed recombination among non-allelic genes was the source. These studies were not designed to estimate recombination loss because the initial level of heterosis could not be established in the absence of the purebred parents and their reciprocal crosses. Furthermore, artificial selection, severe drought conditions and adaptability of specific breeds to the new environment could have also influenced the outcome. Findings described earlier stimulated interest in examining the relationship between heterosis retention and inter-breed recombination among non-allelic genes for performance traits of economical importance in sheep.

In Canada, crossbred evaluation of the Romnelet, Columbia, Suffolk and North Country Cheviot breeds revealed that there was no significant difference between 4-breed and 3-breed crosses for 110 day weaning weight, post-weaning gain and 185 day final market weight (Vesely and Peters, 1979). These results tend to suggest interbreed recombination among non-allelic genes established in specific parental breeds may not be important in the performance of the crossbred individual. In another study, evaluation of the Columbia, Suffolk and Targhee breeds at the University of Minnesota, USA, revealed recombination effects in the crossbred individual for fat depth over loin eye and lower rib, and percentage kidney fat were large though non-significant, but for feed conversion and other carcass traits in the study were negligible (Teehan et al., 1979). Concurrent crossbreeding evaluation at the University of Minnesota, USA for lamb weights at birth and 70 day weaning and age at market weight, and pre- and post-weaning daily gains showed negligible loss from recombination with the exception of age at market weight (Rastogi et al., 1982).

Evaluation of crossbred performance among the Scottish Blackface, Cheviot and Welsh Mountain breeds in the United Kingdom subjected to intense inbreeding revealed heterosis observed in the F₂ generation for body size and conformation, fleece weight and components of fleece, reproductive and maternal performance and lamb survival could not be predicted from performance in the F₁ generation (Weiner and Woolliams, 1980). These results suggest recombination effects may be important. Furthermore, inbreeding of the offspring had a large effect on lamb survival but not prolificacy at birth.

In Spain, the newly developed breed with 50% Romanov and 50% Aragon showed that heterosis retention among generations F₁ to F₆ tended to vary for lamb mortality according to how sheep were raised (Sierra, 1980, 1982). The annual and accelerated lambing system had an important influence on heterosis retention suggesting genotype x environment interaction may be important. At the same time, prolificacy and fecundity were found to be similar between generations F₁ to F₆, indicating recombination loss may not be important for those traits. In France, the newly developed composite population (INRA 401) from the Berrichon du Cher and Romanov breeds, was evaluated from generations F₁ to F₄ and found to remain stable for 30-70 day gain, weight at lambing, fertility, prolificacy and milk production, demonstrating recombination loss may be negligible (Ricordeau et al., 1990). These findings are consistent with increased productivity of Romanov crosses.

Oltenucu and Boylan (1981a,b) evaluated the Finnsheep and Targhee breeds, and Minnesota 100, a composite population (Shrestha et al., 1983) including Finnsheep sired F₁, F₂ and backcrosses at the University of Minnesota, USA for reproduction, lamb survival, lamb weights at birth and weaning, ewe weight and grease fleece weight of ewe lambs and 2-yr old adult ewes. Finnsheep sired Targhee backcrosses exceeded F₂ generation in mean difference for all traits studied except fertility and fecundity of ewe lambs. Similarly Finnsheep sired Suffolk backcross exceeded the F₂ generation in

KEYNOTE ARTICLES

mean difference for all traits except for a modest advantage for lamb mortality, weaning weight and ewe weight, whereas in Finnsheep sired Minnesota 100, F₂ generation was superior or similar to their backcross except for prolificacy of the ewe and fecundity. The mean difference in performance of the F₂ generation and corresponding backcross which provides an estimate of recombination was negligible. Further evidence of a small decline in average performance of Finnsheep sired breed crosses from generations F₁ to F₂ occurred in birth weight, prolificacy, fecundity, grease fleece weight and total lamb weight at weaning per ewe bred except for weaning weight and lamb survival, suggesting recombination effects may be negligible. Similarly, the comparison of generations F₁ and F₂ revealed the decrease in performance was less than what was expected from individual heterozygosity in Finnsheep sired Targhee and Suffolk crosses suggesting negligible loss from recombination except for Finnsheep sired Minnesota 100 crosses. This tends to suggest the parental breeds involved in crossbreeding may influence recombination loss among economically important performance traits.

At the Meat Animal Research Centre, USA, **Fogarty et al. (1984)** evaluated performance of composite populations following *inter se* mating. Composite 1 (½ Finnsheep, ¼ Suffolk and ¼ Targhee) population was bred annually on October whereas Composite 2 (½ Finnsheep, ¼ Dorset and ¼ Rambouillet) population utilized accelerated lambing with breedings in April, August and December. In the annual lambing with October breeding and accelerated lambing with August breeding, heterosis retained in generations F₂ and F₃ was greater than expected from heterozygosity for all traits except lamb survival. In contrast, in accelerated lambing with December breeding, heterosis retained in generations F₂ and F₃ was less than expected from heterozygosity, especially for prolificacy, birth weight and percent alive at birth. This tends to suggest that recombination loss may vary with breeding season because under accelerated lambing two of the three seasons retained more heterosis than expected from heterozygosity.

In Australia, evaluation of the Dorset, Merino and Corriedale breeds, revealed fertility, prolificacy, lamb survival and total lamb weight at weaning per ewe exposed declined from F₁ to F₂ generations (**Ch'ang and Evans, 1986**). The decline for lamb survival and weaning weight was more than expected from heterozygosity suggesting recombination loss, though negligible may be important. At the same time, about one half of the heterosis realized in F₁ was retained in F₂ generation for fertility and fecundity signifying recombination was negligible.

At the Meat Animal Research Centre, USA, **Leymaster cited by Young et al. (1986)** evaluated the Suffolk and Hampshire breeds and their crosses including back cross for reproduction. The average performance of generations F₂ and F₃ as a deviation from F₁ generation and parental pure breeds adjusted for individual and parental heterosis provided an estimate of recombination along with one-half heterosis of maternal effects on ewe performance. It was concluded that recombination effects

between Suffolk and Hampshire breed crosses which may be important for prolificacy at birth was negligible at weaning.

In Morocco, evaluation of the D'man and Sardi breeds revealed fertility, and lamb weights at birth and weaning declined because of recombination loss (Boujenane and Bradford, 1991; Boujenane et al., 1991a,b). In contrast there was no decline for prolificacy and lamb survival indicating loss from recombination was negligible.

In India, evaluation of the Nali breed, along with Merino and Corriedale sired Nali crosses (F₁ and F₂ generations) showed grease fleece weight, staple length, average fibre diameter, and modulation percentage remained stable indicating loss from recombination was negligible (Malik and Singh, 2006). The authors concluded that synthetic population derived from the Nali, Merino and Corriedale breeds following *inter-se* mating in the subsequent generation would remain stable for wool traits because recombination loss was not important.

At the University of Minnesota, USA, performance of Synthetic I (Finnsheep x Lincoln), Synthetic II (Dorset x Rambouillet) and Synthetic III [(Finnsheep x Lincoln) x (Dorset x Rambouillet)] sheep were evaluated following *inter se* mating (Shrestha et al., 2008a,b,c). When the synthetic populations were closed after generation F₄, performance of the synthetic populations as a deviation from the average of their respective purebred parental breeds for body weights of lambs at birth, weaning and at 140d yearling, pre- and post-weaning daily gain, prolificacy, fecundity, lamb survival, wool grade, lamb weights per ewe lambing at weaning and market, milk yield and composition was in the desired direction whereas grease fleece weight and fat content of milk were negligible. These results suggest performance traits of the newly developed synthetic population appeared to retain heterosis, thus recombination loss may be negligible.

DISCUSSION

Evidence substantiating the importance of individual and maternal heterosis for growth, reproduction, wool traits and ewe productivity can be corroborated from a number of studies worldwide (Table 9). These findings confirm heterosis realized from crossing complementary breeds and populations increases productivity. Review of the literature revealed that there was only one estimate of paternal heterosis and none for grand-maternal heterosis. Additional studies need to be carried out to confirm the favourable influence of paternal heterosis. At the same time, if paternal heterosis is important crossbreeding strategies could utilize crossbred rams for commercial sheep production.

Evidence substantiating loss in performance as a result of recombination arising from interbreed recombination among non-allelic genes established in specific parental breeds may be negligible for growth, reproduction, wool traits and ewe productivity can be corroborated from a number of studies worldwide (Table 10). Estimates of recombination loss and heterosis retention in the literature were notably fewer.

KEYNOTE ARTICLES

Although studies described earlier provided estimates of recombination loss for economically important traits, findings were based on small number of animals within purebreds and their crosses. The proportion of resources necessary to estimate recombination loss with a greater deal of precision may be exhaustive. In light of fiscal constraints large expenditure for research in this area would be unlikely. In the present review estimates for heterosis retention were obtained indirectly as mean deviation in performance between generations F₂ and F₁, or deviation in performance of composite population from their respective average performance of purebred parental breeds. **Young et al (1986)** concluded from a review of 20 studies in the literature pertaining to heterosis retention and recombination effects that prediction of heterosis in advanced generations of crossbred population from estimates of initial heterosis and retained heterozyosity may not be accurate in the absence of direct experimentation involving specific breed combinations.

A number of composite populations such as INRA 401 in France derived from the Berrichon du Cher and Romanov breeds (**Ricordeau et al., 1982; Tchamitchian et al., 1986**); new breed in Spain derived from breeds, the Romanov and Aragon (**Sierra, 1980, 1982**); Composite lines 1 and 2 at USDA, USA derived from breeds, the Finnsheep, Rambouillet and Dorset, and the Finnsheep, Suffolk and Targhee, respectively (**Fogarty et al., 1984**); Arcott breeds in Canada derived from multiple breeds e.g. Dorset, East Friesian, Finnsheep, Ile de France, Suffolk, etc. (**Shrestha and Heaney, 2003, 2004**); and Synthetic I and II at the University of Minnesota in USA derived from breeds, the Finnsheep and Lincoln, and the Dorset and Rambouillet, respectively, and Synthetic III derived from the Finnsheep, Lincoln, Dorset and Rambouillet breeds (**Shrestha et al., 2008a,b,c**) have all demonstrated increased productivity. It is likely that crossbreeding in the newly developed breeds may have aided in the fixation of desirable combinations of non-allelic genes established in specific parental breeds. Despite lack of precision, heterosis retention with advancing generations for economically important production traits appear to be in the favourable direction for lamb and ewe productivity, reproduction, and wool traits with the exception of a few traits. Thus there is potential benefit in terms of increased productivity by assembling complementary breeds and populations into composite population. Also genotype x environment interaction has been a concern in a number of studies as many experiments involving imported breeds and their crosses have had their offspring raised in an environment different from those of their imported parental breed. During breed development it is important to consider the accumulation of random changes in gene frequencies over successive generations and the influence of inbreeding on performance of economically important traits by attempting to assemble large number of parents in the foundation flock (**Shrestha et al., 2010**). Nevertheless further studies with large number of sheep breeds and their crosses need to be carried out to confirm the magnitude and direction of recombination loss for economically important performance traits.

Sheep breeders in many parts of the world have opted for mating locally adapted

ewes of the fecund-type dam breed (pure- or crossbred) known to exhibit early maturity and a high frequency of multiple births to rams of the meat-type sire breed with the intention of producing crossbred lambs for market or subsequent breeding under some form of systematic crossbreeding strategy. In practice purebred offspring for herd replacement are retained from approximately one-third of the finest ewe lambs that have survived until breeding age. The remaining selected ewe lambs are bred to rams of an alternate breed purchased from an outstanding breeder to produce crossbred offspring that may be either sold as market lambs, or retained as selected crossbred ewes for subsequent breeding. The operational advantage of crossbreeding lies in retaining the female parent, most likely from an established breed in the region or indigenous population within the farm, while purchasing outstanding male parents from reputable breeders.

Breeders expect the newly developed composite population based on a combination of desirable qualities of two or more breeds to approach the level of performance that could be attained by systematic crossbreeding of two or more breeds, but with a much simpler breeding structure. Additionally, the management of a single population usually has lower requirements for resources and there is no need to purchase new animals, thereby reducing the risk of introducing diseases. Genetic expectation of components pertaining to crossbreeding strategies that include development of composite populations from multiple breeds; specific crosses involving two- or three- or more-breeds; repeated backcrossing of crossbred offspring to the male parent; rotational crossbreeding (or criss-cross) based on two- or more-breeds; and use of a terminal sire breed to produce market lambs from composite population, backcross and rotational cross have been described previously. These expectations demonstrate the inability of offspring derived from backcross, rotational cross and composite population to benefit from genetic superiority associated with the parental breeds plus the full complement of heterosis. This may result from offspring that lack in performance of economically important traits while being less-well-adapted to their new environment. Another approach demonstrating potential merit for increasing productivity is from selection within fecund-type breed sired crossbred populations (Steine, 1985). There is also value in the application of marker assisted selection to genetic evaluation when large numbers of identified markers can improve the accuracy of estimating breeding values. Presently markers identified for wool quality are being utilized for commercial sheep production.

In South Africa, Schoeman et al. (1995) described composite lines recently developed from the Finnsheep and indigenous breeds were comparable with those of the Dorper breed. The authors concluded that composite lines being a small fecund-type dam breed had an advantage for improving biological efficiency within a systematic crossbreeding strategy. Despite the perceived drawback from possible recombination loss, many synthetic breeds that have been developed appear to be promising in terms of increased productivity for economically important traits. These include the development of ABRO Dam line, Cambridge and British Milkshoop in

KEYNOTE ARTICLES

United Kingdom; Fingalway and Improved Galway in Ireland; INRA 401 in France, Coopworth, Souche and Booroola in New Zealand; Gromark in Australia; Arcotts and DLS in Canada; Polypay in USA and many other sheep in the world. In the last century, consumers seeking quality products have had a significant impact on the market resulting in the development of 443 composite breed populations of sheep in 68 countries, all derived from two or more distinct breeds, populations and landraces (Shrestha, 2005).

Breeders, besides having maintained animal populations for a number of years are privy to a wealth of information on their genetic background, health status, behaviour and previously available knowledge on performance. Prospects of utilizing parental breeds or populations carefully selected for crossbreeding depend largely on availability of healthy animals of appropriate breeding age, and most importantly fiscal constraints which usually results in the purchase of a limited number of unrelated animals, mostly sires. There may also be a need to introduce breeding animals and/or fresh and frozen semen as well as embryos chosen for their outstanding inherent genetic potential and as a source of divergent genetic material for crossbreeding. Live animals, embryos and semen with potential merit must meet stringent animal health requirements in the country of origin before an import permit is issued by the importing country. Regulations may vary from country to country according to the status of specific reportable diseases followed by requirement to remain in quarantine for a specified period. This course of action is essential to ensure the health status of the animal industry will not be compromised from introduction of exotic germplasm into the country. Despite sizeable benefits from crossbreeding the availability of healthy animals of prospective breeds within the farm or in close proximity for use as parents, and the order of mating among the pure breeds and their crosses chosen to be sires and dams as well as the operational advantage may dictate the strategy proposed for improvement of productivity in sheep.

In the United Kingdom, regional segmentation of sheep production involves raising Hill breeds in the mountains and 'Down' breeds in the lowlands, which is followed by their crossbreeding to meet the seasonal demand for market lambs. Despite the practical constraints of having to utilize more than two breeds for crossbreeding, substantial gain has been achieved from average breed superiority along with heterosis among complementary breeds. In developing countries, there is no practical evidence of any serious attempt to exploit potential genetic merit among multiple breeds. Considerable opportunity exists in crossing of ewes from indigenous breeds with rams of more productive dairy breeds to produce crossbred ewes with high efficiency in more remote (or tribal) areas for use in terminal crosses under more intensive production close to urban markets.

CONCLUSION

The economic pressure for producing cheaper commodities that began following the

Second World War continues to invigorate interest in attaining optimal productivity. **Carmon et al. (1956)** suggested Rotational crossing can offer an advantage in production performance over the crossing of several breeds followed by random mating. Correspondingly, **Nitter (1978)** concluded from an extensive review of sheep literature, that the Rotational cross may be of higher efficiency relative to specific breed crosses because in the latter approach it is necessary to retain large number of purebred ewes of sub-optimal performance as parental populations for breeding. These findings are in contrast to the belief that specific breed crosses based on crossing fecund-type ewes with meat-type rams can achieve optimal productivity compared to alternate crossbreeding strategies. Although it is vital that breeds with high reproductive rate be included in the crossbreeding strategy, the relative costs in terms of capital expenditure, labour, selection, crossbreeding, breed formation and recurrent crossbreeding for exploitation of heterosis must be assessed before making a decision on a particular strategy for commercial production. Furthermore, in developing countries improved and indigenous sheep and their crosses need to be evaluated in relation to religious rituals, socio-economic value, fiscal constraints and limitations. The development of composite populations based on combination of exotic breeds with outstanding performance and indigenous populations with adaptability demonstrate considerable potential for increasing productivity. Finally the choice of crossbreeding strategy that would be beneficial to sheep producers from increased productivity would depend on their willingness to apply innovative breeding methods. Important concerns that need to be addressed are operational aspects, lower requirements for resources such as availability of animals of a specific breed or breed crosses within farm premises with no need to purchase new animals thereby reducing the risk of introducing diseases, proximity to markets and distribution, access to credit, expert professional advice, harmony with culture and religious rituals. The application of crossbreeding strategies based on quantitative genetic principles for exploiting sheep genetic resources worldwide demonstrate sizeable benefit from individual and maternal heterosis with negligible loss from recombination enhancing prospect for attaining increased productivity.

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KEYNOTE ARTICLES

Table 1. Theoretical expectations for Purebred, Single-cross (F₁), F₂ and F₃ mating.

Mating		Individual			Maternal		Paternal		Grand-maternal			Genetic	Heterosis
Sire	Dam	Genetic	Heterosis	Recom.	Genetic	Heterosis	Recom.	Genetic	Heterosis	Recom.			
Purebred													
A	A	g_A^I	•	•	g_A^M	•	•	g_A^P	•	•	g_A^M	•	•
B	B	g_B^I	•	•	g_B^M	•	•	g_B^P	•	•	g_B^M	•	•
C	C	g_C^I	•	•	g_C^M	•	•	g_C^P	•	•	g_C^M	•	•
D	D	g_D^I	•	•	g_D^M	•	•	g_D^P	•	•	g_D^M	•	•
Single cross (F₁)													
A	B	$\frac{1}{2}(g_A^I + g_B^I)$	h_{AB}^I	•	g_B^M	•	•	g_A^P	•	•	g_B^M	•	•
B	A	$\frac{1}{2}(g_B^I + g_A^I)$	h_{BA}^I	•	g_A^M	•	•	g_B^P	•	•	g_A^M	•	•
A	C	$\frac{1}{2}(g_A^I + g_C^I)$	h_{AC}^I	•	g_C^M	•	•	g_A^P	•	•	g_C^M	•	•
C	A	$\frac{1}{2}(g_C^I + g_A^I)$	h_{CA}^I	•	g_A^M	•	•	g_C^P	•	•	g_A^M	•	•
A	D	$\frac{1}{2}(g_A^I + g_D^I)$	h_{AD}^I	•	g_D^M	•	•	g_A^P	•	•	g_D^M	•	•
D	A	$\frac{1}{2}(g_D^I + g_A^I)$	h_{DA}^I	•	g_A^M	•	•	g_D^P	•	•	g_A^M	•	•
B	C	$\frac{1}{2}(g_B^I + g_C^I)$	h_{BC}^I	•	g_C^M	•	•	g_B^P	•	•	g_C^M	•	•
C	B	$\frac{1}{2}(g_C^I + g_B^I)$	h_{CB}^I	•	g_B^M	•	•	g_C^P	•	•	g_B^M	•	•
F₂													
(AxB)	(AxB)	$\frac{1}{2}(g_A^I + g_B^I)$	$\frac{1}{2}h_{AB}^I$	r_{AB}^I	$\frac{1}{2}(g_A^M + g_B^M)$	h_{AB}^M	•	$\frac{1}{2}(g_A^P + g_B^P)$	h_{AB}^P	•	g_B^M	•	•
(AxC)	(AxC)	$\frac{1}{2}(g_A^I + g_C^I)$	$\frac{1}{2}h_{AC}^I$	r_{AC}^I	$\frac{1}{2}(g_A^M + g_C^M)$	h_{AC}^M	•	$\frac{1}{2}(g_A^P + g_C^P)$	h_{AC}^P	•	g_C^M	•	•
(AxD)	(AxD)	$\frac{1}{2}(g_A^I + g_D^I)$	$\frac{1}{2}h_{AD}^I$	r_{AD}^I	$\frac{1}{2}(g_A^M + g_D^M)$	h_{AD}^M	•	$\frac{1}{2}(g_A^P + g_D^P)$	h_{AD}^P	•	g_D^M	•	•
(BxC)	(BxC)	$\frac{1}{2}(g_B^I + g_C^I)$	$\frac{1}{2}h_{BC}^I$	r_{BC}^I	$\frac{1}{2}(g_B^M + g_C^M)$	h_{BC}^M	•	$\frac{1}{2}(g_B^P + g_C^P)$	h_{BC}^P	•	g_C^M	•	•
F₃													
(AxB) ²	(AxB) ²	$\frac{1}{2}(g_A^I + g_B^I)$	$\frac{1}{2}h_{AB}^I$	r_{AB}^I	$\frac{1}{2}(g_A^M + g_B^M)$	$\frac{1}{2}h_{AB}^M$	r_{AB}^M	$\frac{1}{2}(g_A^P + g_B^P)$	$\frac{1}{2}h_{AB}^P$	r_{AB}^P	$\frac{1}{2}(g_A^M + g_B^M)$	h_{AB}^M	h_{AB}^M
(AxC) ²	(AxC) ²	$\frac{1}{2}(g_A^I + g_C^I)$	$\frac{1}{2}h_{AC}^I$	r_{AC}^I	$\frac{1}{2}(g_A^M + g_C^M)$	$\frac{1}{2}h_{AC}^M$	r_{AC}^M	$\frac{1}{2}(g_A^P + g_C^P)$	$\frac{1}{2}h_{AC}^P$	r_{AC}^P	$\frac{1}{2}(g_A^M + g_C^M)$	h_{AC}^M	h_{AC}^M
(AxD) ²	(AxD) ²	$\frac{1}{2}(g_A^I + g_D^I)$	$\frac{1}{2}h_{AD}^I$	r_{AD}^I	$\frac{1}{2}(g_A^M + g_D^M)$	$\frac{1}{2}h_{AD}^M$	r_{AD}^M	$\frac{1}{2}(g_A^P + g_D^P)$	$\frac{1}{2}h_{AD}^P$	r_{AD}^P	$\frac{1}{2}(g_A^M + g_D^M)$	h_{AD}^M	h_{AD}^M
(BxC) ²	(BxC) ²	$\frac{1}{2}(g_B^I + g_C^I)$	$\frac{1}{2}h_{BC}^I$	r_{BC}^I	$\frac{1}{2}(g_B^M + g_C^M)$	$\frac{1}{2}h_{BC}^M$	r_{BC}^M	$\frac{1}{2}(g_B^P + g_C^P)$	$\frac{1}{2}h_{BC}^P$	r_{BC}^P	$\frac{1}{2}(g_B^M + g_C^M)$	h_{BC}^M	h_{BC}^M

Table 2. Theoretical expectations for Back-cross (BC₁, BC₂ and BC₃) mating.

Sire	Dam	Individual			Maternal			Paternal	Grand-maternal		
		Genetic	Heterosis	Recom.	Genetic	Heterosis	Recom.	Genetic	Genetic	Heterosis	Recom.
Backcross (BC₁) mating											
A	AxB	$\frac{3}{4}g_A^i + \frac{1}{4}g_B^i$	$\frac{1}{2}h_{AB}^i$	$\frac{1}{2}r_{AB}^i$	$\frac{1}{2}(g_A^M + g_B^M)$	h_{AB}^M	.	g_A^P	g_B^M	.	.
B	BxA	$\frac{3}{4}g_B^i + \frac{1}{4}g_A^i$	$\frac{1}{2}h_{BA}^i$	$\frac{1}{2}r_{BA}^i$	$\frac{1}{2}(g_B^M + g_A^M)$	h_{BA}^M	.	g_B^P	g_A^M	.	.
A	AxC	$\frac{3}{4}g_A^i + \frac{1}{4}g_C^i$	$\frac{1}{2}h_{AC}^i$	$\frac{1}{2}r_{AC}^i$	$\frac{1}{2}(g_A^M + g_C^M)$	h_{AC}^M	.	g_A^P	g_C^M	.	.
C	CxA	$\frac{3}{4}g_C^i + \frac{1}{4}g_A^i$	$\frac{1}{2}h_{CA}^i$	$\frac{1}{2}r_{CA}^i$	$\frac{1}{2}(g_C^M + g_A^M)$	h_{CA}^M	.	g_C^P	g_A^M	.	.
A	AxD	$\frac{3}{4}g_A^i + \frac{1}{4}g_D^i$	$\frac{1}{2}h_{AD}^i$	$\frac{1}{2}r_{AD}^i$	$\frac{1}{2}(g_A^M + g_D^M)$	h_{AD}^M	.	g_A^P	g_D^M	.	.
D	DxA	$\frac{3}{4}g_D^i + \frac{1}{4}g_A^i$	$\frac{1}{2}h_{DA}^i$	$\frac{1}{2}r_{DA}^i$	$\frac{1}{2}(g_D^M + g_A^M)$	h_{DA}^M	.	g_D^P	g_A^M	.	.
Backcross (BC₂) mating											
A	Ax(AxB)	$\frac{7}{8}g_A^i + \frac{1}{8}g_B^i$	$\frac{1}{4}h_{AB}^i$	$\frac{1}{4}r_{AB}^i$	$\frac{3}{4}g_A^M + \frac{1}{4}g_B^M$	$\frac{1}{2}h_{AB}^M$	$\frac{1}{2}r_{AB}^M$	g_A^P	$\frac{1}{2}(g_A^M + g_B^M)$	h_{AB}^M	.
B	Bx(BxA)	$\frac{7}{8}g_B^i + \frac{1}{8}g_A^i$	$\frac{1}{4}h_{BA}^i$	$\frac{1}{4}r_{BA}^i$	$\frac{3}{4}g_B^M + \frac{1}{4}g_A^M$	$\frac{1}{2}h_{BA}^M$	$\frac{1}{2}r_{BA}^M$	g_B^P	$\frac{1}{2}(g_B^M + g_A^M)$	h_{BA}^M	.
A	Ax(AxC)	$\frac{7}{8}g_A^i + \frac{1}{8}g_C^i$	$\frac{1}{4}h_{AC}^i$	$\frac{1}{4}r_{AC}^i$	$\frac{3}{4}g_A^M + \frac{1}{4}g_C^M$	$\frac{1}{2}h_{AC}^M$	$\frac{1}{2}r_{AC}^M$	g_A^P	$\frac{1}{2}(g_A^M + g_C^M)$	h_{AC}^M	.
C	Cx(CxA)	$\frac{7}{8}g_C^i + \frac{1}{8}g_A^i$	$\frac{1}{4}h_{CA}^i$	$\frac{1}{4}r_{CA}^i$	$\frac{3}{4}g_C^M + \frac{1}{4}g_A^M$	$\frac{1}{2}h_{CA}^M$	$\frac{1}{2}r_{CA}^M$	g_C^P	$\frac{1}{2}(g_C^M + g_A^M)$	h_{CA}^M	.
A	Ax(AxD)	$\frac{7}{8}g_A^i + \frac{1}{8}g_D^i$	$\frac{1}{4}h_{AD}^i$	$\frac{1}{4}r_{AD}^i$	$\frac{3}{4}g_A^M + \frac{1}{4}g_D^M$	$\frac{1}{2}h_{AD}^M$	$\frac{1}{2}r_{AD}^M$	g_A^P	$\frac{1}{2}(g_A^M + g_D^M)$	h_{AD}^M	.
D	Dx(DxA)	$\frac{7}{8}g_D^i + \frac{1}{8}g_A^i$	$\frac{1}{4}h_{DA}^i$	$\frac{1}{4}r_{DA}^i$	$\frac{3}{4}g_D^M + \frac{1}{4}g_A^M$	$\frac{1}{2}h_{DA}^M$	$\frac{1}{2}r_{DA}^M$	g_D^P	$\frac{1}{2}(g_D^M + g_A^M)$	h_{DA}^M	.
Backcross (BC₃) mating											
A	A{Ax(AxB)}	$\frac{15}{16}g_A^i + \frac{1}{16}g_B^i$	$\frac{1}{8}h_{AB}^i$	$\frac{1}{8}r_{AB}^i$	$\frac{7}{8}g_A^M + \frac{1}{8}g_B^M$	$\frac{1}{4}h_{AB}^M$	$\frac{1}{4}r_{AB}^M$	g_A^P	$\frac{3}{4}g_A^M + \frac{1}{4}g_B^M$	$\frac{1}{2}h_{AB}^M$	$\frac{1}{2}r_{AB}^M$
B	B{Bx(BxA)}	$\frac{15}{16}g_B^i + \frac{1}{16}g_A^i$	$\frac{1}{8}h_{BA}^i$	$\frac{1}{8}r_{BA}^i$	$\frac{7}{8}g_B^M + \frac{1}{8}g_A^M$	$\frac{1}{4}h_{BA}^M$	$\frac{1}{4}r_{BA}^M$	g_B^P	$\frac{3}{4}g_B^M + \frac{1}{4}g_A^M$	$\frac{1}{2}h_{BA}^M$	$\frac{1}{2}r_{BA}^M$
A	A{Ax(AxC)}	$\frac{15}{16}g_A^i + \frac{1}{16}g_C^i$	$\frac{1}{8}h_{AC}^i$	$\frac{1}{8}r_{AC}^i$	$\frac{7}{8}g_A^M + \frac{1}{8}g_C^M$	$\frac{1}{4}h_{AC}^M$	$\frac{1}{4}r_{AC}^M$	g_A^P	$\frac{3}{4}g_A^M + \frac{1}{4}g_C^M$	$\frac{1}{2}h_{AC}^M$	$\frac{1}{2}r_{AC}^M$
C	C{Cx(CxA)}	$\frac{15}{16}g_C^i + \frac{1}{16}g_A^i$	$\frac{1}{8}h_{CA}^i$	$\frac{1}{8}r_{CA}^i$	$\frac{7}{8}g_C^M + \frac{1}{8}g_A^M$	$\frac{1}{4}h_{CA}^M$	$\frac{1}{4}r_{CA}^M$	g_C^P	$\frac{3}{4}g_C^M + \frac{1}{4}g_A^M$	$\frac{1}{2}h_{CA}^M$	$\frac{1}{2}r_{CA}^M$
A	A{Ax(AxD)}	$\frac{15}{16}g_A^i + \frac{1}{16}g_D^i$	$\frac{1}{8}h_{AD}^i$	$\frac{1}{8}r_{AD}^i$	$\frac{7}{8}g_A^M + \frac{1}{8}g_D^M$	$\frac{1}{4}h_{AD}^M$	$\frac{1}{4}r_{AD}^M$	g_A^P	$\frac{3}{4}g_A^M + \frac{1}{4}g_D^M$	$\frac{1}{2}h_{AD}^M$	$\frac{1}{2}r_{AD}^M$
D	D{Dx(DxA)}	$\frac{15}{16}g_D^i + \frac{1}{16}g_A^i$	$\frac{1}{8}h_{DA}^i$	$\frac{1}{8}r_{DA}^i$	$\frac{7}{8}g_D^M + \frac{1}{8}g_A^M$	$\frac{1}{4}h_{DA}^M$	$\frac{1}{4}r_{DA}^M$	g_D^P	$\frac{3}{4}g_D^M + \frac{1}{4}g_A^M$	$\frac{1}{2}h_{DA}^M$	$\frac{1}{2}r_{DA}^M$

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Table 3. Theoretical expectations for specific three- and four-breed cross mating.

Mating		Individual			Maternal		Paternal		Grand-maternal
Sire	Dam	Genetic	Heterosis	Recom.	Genetic	Heterosis	Genetic	Heterosis	Genetic
Specific three-breed cross mating									
A	BxD	$\frac{1}{2} g'_A + \frac{1}{4} (g'_B + g'_D)$	$\frac{1}{2} (h'_{AB} + h'_{AD})$	$\frac{1}{2} r'_{BD}$	$\frac{1}{2} (g^M_B + g^M_D)$	h^M_{BD}	g^P_A	•	g^M_D
A	CxD	$\frac{1}{2} g'_A + \frac{1}{4} (g'_C + g'_D)$	$\frac{1}{2} (h'_{AC} + h'_{AD})$	$\frac{1}{2} r'_{CD}$	$\frac{1}{2} (g^M_C + g^M_D)$	h^M_{CD}	g^P_A	•	g^M_D
B	AxC	$\frac{1}{2} g'_B + \frac{1}{4} (g'_A + g'_C)$	$\frac{1}{2} (h'_{BA} + h'_{BC})$	$\frac{1}{2} r'_{AC}$	$\frac{1}{2} (g^M_A + g^M_C)$	h^M_{AC}	g^P_B	•	g^M_C
B	CxD	$\frac{1}{2} g'_B + \frac{1}{4} (g'_C + g'_D)$	$\frac{1}{2} (h'_{BC} + h'_{BD})$	$\frac{1}{2} r'_{CD}$	$\frac{1}{2} (g^M_C + g^M_D)$	h^M_{CD}	g^P_B	•	g^M_D
C	AxB	$\frac{1}{2} g'_C + \frac{1}{4} (g'_A + g'_B)$	$\frac{1}{2} (h'_{CA} + h'_{CB})$	$\frac{1}{2} r'_{AB}$	$\frac{1}{2} (g^M_A + g^M_B)$	h^M_{AB}	g^P_C	•	g^M_B
C	BxD	$\frac{1}{2} g'_C + \frac{1}{4} (g'_B + g'_D)$	$\frac{1}{2} (h'_{CB} + h'_{CD})$	$\frac{1}{2} r'_{BD}$	$\frac{1}{2} (g^M_B + g^M_D)$	h^M_{BD}	g^P_C	•	g^M_D
D	AxB	$\frac{1}{2} g'_D + \frac{1}{4} (g'_A + g'_B)$	$\frac{1}{2} (h'_{DA} + h'_{DB})$	$\frac{1}{2} r'_{AB}$	$\frac{1}{2} (g^M_A + g^M_B)$	h^M_{AB}	g^P_D	•	g^M_B
D	AxC	$\frac{1}{2} g'_D + \frac{1}{4} (g'_A + g'_C)$	$\frac{1}{2} (h'_{DA} + h'_{DC})$	$\frac{1}{2} r'_{AC}$	$\frac{1}{2} (g^M_A + g^M_C)$	h^M_{AC}	g^P_D	•	g^M_C
BxD	A	$\frac{1}{4} (g'_B + g'_D) + \frac{1}{2} g'_A$	$\frac{1}{2} (h'_{BA} + h'_{DA})$	$\frac{1}{2} r'_{BD}$	g^M_A	•	$\frac{1}{2} (g^P_B + g^P_D)$	h^P_{BD}	g^M_A
CxD	A	$\frac{1}{4} (g'_C + g'_D) + \frac{1}{2} g'_A$	$\frac{1}{2} (h'_{CA} + h'_{DA})$	$\frac{1}{2} r'_{CD}$	g^M_A	•	$\frac{1}{2} (g^P_C + g^P_D)$	h^P_{CD}	g^M_A
AxC	B	$\frac{1}{4} (g'_A + g'_C) + \frac{1}{2} g'_B$	$\frac{1}{2} (h'_{AB} + h'_{CB})$	$\frac{1}{2} r'_{AC}$	g^M_B	•	$\frac{1}{2} (g^P_A + g^P_C)$	h^P_{AC}	g^M_B
CxD	B	$\frac{1}{4} (g'_C + g'_D) + \frac{1}{2} g'_B$	$\frac{1}{2} (h'_{CB} + h'_{DB})$	$\frac{1}{2} r'_{CD}$	g^M_B	•	$\frac{1}{2} (g^P_C + g^P_D)$	h^P_{CD}	g^M_B
AxB	C	$\frac{1}{4} (g'_A + g'_B) + \frac{1}{2} g'_C$	$\frac{1}{2} (h'_{AC} + h'_{BC})$	$\frac{1}{2} r'_{AB}$	g^M_C	•	$\frac{1}{2} (g^P_A + g^P_B)$	h^P_{AB}	g^M_C
BxD	C	$\frac{1}{4} (g'_B + g'_D) + \frac{1}{2} g'_C$	$\frac{1}{2} (h'_{BC} + h'_{DC})$	$\frac{1}{2} r'_{BD}$	g^M_C	•	$\frac{1}{2} (g^P_B + g^P_D)$	h^P_{BD}	g^M_C
AxB	D	$\frac{1}{4} (g'_A + g'_B) + \frac{1}{2} g'_D$	$\frac{1}{2} (h'_{AD} + h'_{BD})$	$\frac{1}{2} r'_{AB}$	g^M_D	•	$\frac{1}{2} (g^P_A + g^P_B)$	h^P_{AB}	g^M_D
AxC	D	$\frac{1}{4} (g'_A + g'_C) + \frac{1}{2} g'_D$	$\frac{1}{2} (h'_{AD} + h'_{CD})$	$\frac{1}{2} r'_{AC}$	g^M_D	•	$\frac{1}{2} (g^P_A + g^P_C)$	h^P_{AC}	g^M_D
Specific four-breed cross mating									
AxB	CxD	$\frac{1}{4} (g'_A + g'_B + g'_C + g'_D)$	$\frac{1}{4} (h'_{AC} + h'_{AD} + h'_{BC} + h'_{BD})$	$\frac{1}{2} r'_{CD}$	$\frac{1}{2} (g^M_C + g^M_D)$	h^M_{CD}	$\frac{1}{2} (g^P_A + g^P_B)$	h^P_{AB}	g^M_D
CxD	AxB	$\frac{1}{4} (g'_C + g'_D + g'_A + g'_B)$	$\frac{1}{4} (h'_{CA} + h'_{CB} + h'_{DA} + h'_{DB})$	$\frac{1}{2} r'_{AB}$	$\frac{1}{2} (g^M_A + g^M_B)$	h^M_{AB}	$\frac{1}{2} (g^P_C + g^P_D)$	h^P_{CD}	g^M_B
AxC	BxD	$\frac{1}{4} (g'_A + g'_C + g'_B + g'_D)$	$\frac{1}{4} (h'_{AB} + h'_{AD} + h'_{CB} + h'_{CD})$	$\frac{1}{2} r'_{BD}$	$\frac{1}{2} (g^M_B + g^M_D)$	h^M_{BD}	$\frac{1}{2} (g^P_A + g^P_C)$	h^P_{AC}	g^M_D
BxD	AxC	$\frac{1}{4} (g'_B + g'_D + g'_A + g'_C)$	$\frac{1}{4} (h'_{BA} + h'_{BC} + h'_{DA} + h'_{DC})$	$\frac{1}{2} r'_{AC}$	$\frac{1}{2} (g^M_A + g^M_C)$	h^M_{AC}	$\frac{1}{2} (g^P_B + g^P_D)$	h^P_{BD}	g^M_C

3rd International Scientific Conference on Small Ruminant Development, Hurghada, Egypt, 12-15 April, 2010

Table 4. Theoretical expectations for two-, three- and four-breed Rotational cross mating (with equal proportion of breeds). (shaded raw is continuation of every previously located raw).

Effects	Two-breed Rotation				Three-breed Rotation	
	[A-B]	[A-C]	[A-D]	[B-C]	[A-B-C]	[A-B-D]
	Three-breed Rotation			Four-breed Rotation		
	[B-C-D]			[A-B-C-D]		
Individual						
Genetic	$\frac{1}{2}(g_A^I + g_B^I)$	$\frac{1}{2}(g_A^I + g_C^I)$	$\frac{1}{2}(g_A^I + g_D^I)$	$\frac{1}{2}(g_B^I + g_C^I)$	$\frac{1}{3}(g_A^I + g_B^I + g_C^I)$	$\frac{1}{3}(g_A^I + g_B^I + g_D^I)$
	$\frac{1}{3}(g_A^I + g_C^I + g_D^I)$			$\frac{1}{4}(g_A^I + g_B^I + g_C^I + g_D^I)$		
Heterosis	$\frac{2}{3}h_{AB}^I$	$\frac{2}{3}h_{AC}^I$	$\frac{2}{3}h_{AD}^I$	$\frac{2}{3}h_{BC}^I$	$\frac{6}{21}(h_{AB}^I + h_{AC}^I + h_{BC}^I)$	$\frac{6}{21}(h_{AB}^I + h_{AD}^I + h_{BD}^I)$
	$\frac{6}{21}(h_{AC}^I + h_{AD}^I + h_{CD}^I)$			$\frac{6}{21}(h_{AB}^I + h_{AC}^I + h_{AD}^I + h_{BC}^I + h_{BD}^I + h_{CD}^I)$		
Recom.	$\frac{1}{3}r_{AB}^I$	$\frac{1}{3}r_{AC}^I$	$\frac{1}{3}r_{AD}^I$	$\frac{1}{3}r_{BC}^I$	$\frac{3}{21}(r_{AB}^I + r_{AC}^I + r_{BC}^I)$	$\frac{3}{21}(r_{AB}^I + r_{AD}^I + r_{BD}^I)$
	$\frac{1}{21}(r_{BC}^I + r_{BD}^I + r_{CD}^I)$			$\frac{7}{90}(r_{AB}^I + r_{AC}^I + r_{AD}^I + r_{BC}^I + r_{BD}^I + r_{CD}^I)$		
Maternal						
Genetic	$\frac{1}{2}(g_A^M + g_B^M)$	$\frac{1}{2}(g_A^M + g_C^M)$	$\frac{1}{2}(g_A^M + g_D^M)$	$\frac{1}{2}(g_B^M + g_C^M)$	$\frac{1}{3}(g_A^M + g_B^M + g_C^M)$	$\frac{1}{3}(g_A^M + g_B^M + g_D^M)$
	$\frac{1}{3}(g_A^M + g_C^M + g_D^M)$			$\frac{1}{4}(g_A^M + g_B^M + g_C^M + g_D^M)$		
Heterosis	$\frac{2}{3}h_{AB}^M$	$\frac{2}{3}h_{AC}^M$	$\frac{2}{3}h_{AD}^M$	$\frac{2}{3}h_{BC}^M$	$\frac{6}{21}(h_{AB}^M + h_{AC}^M + h_{BC}^M)$	$\frac{6}{21}(h_{AB}^M + h_{AD}^M + h_{BD}^M)$
	$\frac{6}{21}(h_{AC}^M + h_{AD}^M + h_{CD}^M)$			$\frac{6}{21}(h_{AB}^M + h_{AC}^M + h_{AD}^M + h_{BC}^M + h_{BD}^M + h_{CD}^M)$		
Recom.	$\frac{1}{3}r_{AB}^M$	$\frac{1}{3}r_{AC}^M$	$\frac{1}{3}r_{AD}^M$	$\frac{1}{3}r_{BC}^M$	$\frac{3}{21}(r_{AB}^M + r_{AC}^M + r_{BC}^M)$	$\frac{3}{21}(r_{AB}^M + r_{AD}^M + r_{BD}^M)$
	$\frac{1}{21}(r_{BC}^M + r_{BD}^M + r_{CD}^M)$			$\frac{7}{90}(r_{AB}^M + r_{AC}^M + r_{AD}^M + r_{BC}^M + r_{BD}^M + r_{CD}^M)$		
Paternal						
Genetic	$\frac{1}{2}(g_A^P + g_B^P)$	$\frac{1}{2}(g_A^P + g_C^P)$	$\frac{1}{2}(g_A^P + g_D^P)$	$\frac{1}{2}(g_B^P + g_C^P)$	$\frac{1}{3}(g_A^P + g_B^P + g_C^P)$	$\frac{1}{3}(g_A^P + g_B^P + g_D^P)$
	$\frac{1}{3}(g_A^P + g_C^P + g_D^P)$			$\frac{1}{4}(g_A^P + g_B^P + g_C^P + g_D^P)$		
Grand-maternal						
Genetic	$\frac{1}{2}(g_A^M + g_B^M)$	$\frac{1}{2}(g_A^M + g_C^M)$	$\frac{1}{2}(g_A^M + g_D^M)$	$\frac{1}{2}(g_B^M + g_C^M)$	$\frac{1}{3}(g_A^M + g_B^M + g_C^M)$	$\frac{1}{3}(g_A^M + g_B^M + g_D^M)$
	$\frac{1}{3}(g_A^M + g_C^M + g_D^M)$			$\frac{1}{4}(g_A^M + g_B^M + g_C^M + g_D^M)$		
Heterosis	$\frac{2}{3}h_{AB}^M$	$\frac{2}{3}h_{AC}^M$	$\frac{2}{3}h_{AD}^M$	$\frac{2}{3}h_{BC}^M$	$\frac{6}{21}(h_{AB}^M + h_{AC}^M + h_{BC}^M)$	$\frac{6}{21}(h_{AB}^M + h_{AD}^M + h_{BD}^M)$
	$\frac{6}{21}(h_{AC}^M + h_{AD}^M + h_{CD}^M)$			$\frac{6}{21}(h_{AB}^M + h_{AC}^M + h_{AD}^M + h_{BC}^M + h_{BD}^M + h_{CD}^M)$		
Recom.	$\frac{1}{3}r_{AB}^M$	$\frac{1}{3}r_{AC}^M$	$\frac{1}{3}r_{AD}^M$	$\frac{1}{3}r_{BC}^M$	$\frac{3}{21}(r_{AB}^M + r_{AC}^M + r_{BC}^M)$	$\frac{3}{21}(r_{AB}^M + r_{AD}^M + r_{BD}^M)$
	$\frac{1}{21}(r_{BC}^M + r_{BD}^M + r_{CD}^M)$			$\frac{7}{90}(r_{AB}^M + r_{AC}^M + r_{AD}^M + r_{BC}^M + r_{BD}^M + r_{CD}^M)$		

KEYNOTE ARTICLES

Table 5. Theoretical expectations for two-, three- and four breed Synthetic population (with equal proportion of breeds). (Note: Every shaded row is a continuation of the previous row to it)

Effects	Two-breed Synthetic				Three-breed Synthetic	
	[A:B]	[A:C]	[A:D]	[B:C]	[A:B:C]	[A:B:D]
	Two-breed Synthetic				Three-breed Synthetic	
	[A:C]	[A:D]	[A:B:C:D]			
Individual						
Genetic	$\frac{1}{2}(g'_A + g'_B)$	$\frac{1}{2}(g'_A + g'_C)$	$\frac{1}{2}(g'_A + g'_D)$	$\frac{1}{2}(g'_B + g'_C)$	$\frac{1}{3}(g'_A + g'_B + g'_C)$	$\frac{1}{3}(g'_A + g'_B + g'_D)$
	$\frac{1}{3}(g'_B + g'_C + g'_D)$			$\frac{1}{4}(g'_A + g'_B + g'_C + g'_D)$		
Heterosis	$\frac{1}{2}h'_{AB}$	$\frac{1}{2}h'_{AC}$	$\frac{1}{2}h'_{AD}$	$\frac{1}{2}h'_{BC}$	$\frac{2}{9}(h'_{AB} + h'_{AC} + h'_{BC})$	$\frac{2}{9}(h'_{AB} + h'_{AD} + h'_{BD})$
	$\frac{2}{9}(h'_{BC} + h'_{BD} + h'_{CD})$			$\frac{3}{24}(h'_{AB} + h'_{AC} + h'_{AD} + h'_{BC} + h'_{BD} + h'_{CD})$		
Recom.	$\frac{1}{2}r'_{AB}$	$\frac{1}{2}r'_{AC}$	$\frac{1}{2}r'_{AD}$	$\frac{1}{2}r'_{BC}$	$\frac{2}{9}(r'_{AB} + r'_{AC} + r'_{BC})$	$\frac{2}{9}(r'_{AB} + r'_{AD} + r'_{BD})$
	$\frac{2}{9}(r'_{BC} + r'_{BD} + r'_{CD})$			$\frac{3}{24}(r'_{AB} + r'_{AC} + r'_{AD} + r'_{BC} + r'_{BD} + r'_{CD})$		
Maternal						
Genetic	$\frac{1}{2}(g^M_A + g^M_B)$	$\frac{1}{2}(g^M_A + g^M_C)$	$\frac{1}{2}(g^M_A + g^M_D)$	$\frac{1}{2}(g^M_B + g^M_C)$	$\frac{1}{3}(g^M_A + g^M_B + g^M_C)$	$\frac{1}{3}(g^M_A + g^M_B + g^M_D)$
	$\frac{1}{3}(g^M_B + g^M_C + g^M_D)$			$\frac{1}{4}(g^M_A + g^M_B + g^M_C + g^M_D)$		
Heterosis	$\frac{1}{2}h^M_{AB}$	$\frac{1}{2}h^M_{AC}$	$\frac{1}{2}h^M_{AD}$	$\frac{1}{2}h^M_{BC}$	$\frac{2}{9}(h^M_{AB} + h^M_{AC} + h^M_{BC})$	$\frac{2}{9}(h^M_{AB} + h^M_{AD} + h^M_{BD})$
	$\frac{2}{9}(h^M_{BC} + h^M_{BD} + h^M_{CD})$			$\frac{3}{24}(h^M_{AB} + h^M_{AC} + h^M_{AD} + h^M_{BC} + h^M_{BD} + h^M_{CD})$		
Recom.	$\frac{1}{2}r^M_{AB}$	$\frac{1}{2}r^M_{AC}$	$\frac{1}{2}r^M_{AD}$	$\frac{1}{2}r^M_{BC}$	$\frac{2}{9}(r^M_{AB} + r^M_{AC} + r^M_{BC})$	$\frac{2}{9}(r^M_{AB} + r^M_{AD} + r^M_{BD})$
	$\frac{2}{9}(r^M_{BC} + r^M_{BD} + r^M_{CD})$			$\frac{3}{24}(r^M_{AB} + r^M_{AC} + r^M_{AD} + r^M_{BC} + r^M_{BD} + r^M_{CD})$		
Paternal						
Genetic	$\frac{1}{2}(g^P_A + g^P_B)$	$\frac{1}{2}(g^P_A + g^P_C)$	$\frac{1}{2}(g^P_A + g^P_D)$	$\frac{1}{2}(g^P_B + g^P_C)$	$\frac{1}{3}(g^P_A + g^P_B + g^P_C)$	$\frac{1}{3}(g^P_A + g^P_B + g^P_D)$
	$\frac{1}{3}(g^P_B + g^P_C + g^P_D)$			$\frac{1}{4}(g^P_A + g^P_B + g^P_C + g^P_D)$		
Heterosis	$\frac{1}{2}h^P_{AB}$	$\frac{1}{2}h^P_{AC}$	$\frac{1}{2}h^P_{AD}$	$\frac{1}{2}h^P_{BC}$	$\frac{2}{9}(h^P_{AB} + h^P_{AC} + h^P_{BC})$	$\frac{2}{9}(h^P_{AB} + h^P_{AD} + h^P_{BD})$
	$\frac{2}{9}(h^P_{BC} + h^P_{BD} + h^P_{CD})$			$\frac{3}{24}(h^P_{AB} + h^P_{AC} + h^P_{AD} + h^P_{BC} + h^P_{BD} + h^P_{CD})$		
Recom.	$\frac{1}{2}r^P_{AB}$	$\frac{1}{2}r^P_{AC}$	$\frac{1}{2}r^P_{AD}$	$\frac{1}{2}r^P_{BC}$	$\frac{2}{9}(r^P_{AB} + r^P_{AC} + r^P_{BC})$	$\frac{2}{9}(r^P_{AB} + r^P_{AD} + r^P_{BD})$
	$\frac{2}{9}(r^P_{BC} + r^P_{BD} + r^P_{CD})$			$\frac{3}{24}(r^P_{AB} + r^P_{AC} + r^P_{AD} + r^P_{BC} + r^P_{BD} + r^P_{CD})$		

3rd International Scientific Conference on Small Ruminant Development, Hurghada, Egypt, 12-15 April, 2010

Grand-maternal

Genetic	$\frac{1}{2}(g_A^{M'} + g_B^{M'})$	$\frac{1}{2}(g_A^{M'} + g_C^{M'})$	$\frac{1}{2}(g_A^{M'} + g_D^{M'})$	$\frac{1}{2}(g_B^{M'} + g_C^{M'})$	$\frac{1}{3}(g_A^{M'} + g_B^{M'} + g_C^{M'})$	$\frac{1}{3}(g_A^{M'} + g_B^{M'} + g_D^{M'})$
	$\frac{1}{3}(g_B^{M'} + g_C^{M'} + g_D^{M'})$			$\frac{1}{4}(g_A^{M'} + g_B^{M'} + g_C^{M'} + g_D^{M'})$		
Heterosis	$\frac{1}{2}h_{AB}^{M'}$	$\frac{1}{2}h_{AC}^{M'}$	$\frac{1}{2}h_{AD}^{M'}$	$\frac{1}{2}h_{BC}^{M'}$	$\frac{2}{9}(h_{AB}^{M'} + h_{AC}^{M'} + h_{BC}^{M'})$	$\frac{2}{9}(h_{AB}^{M'} + h_{AD}^{M'} + h_{BD}^{M'})$
	$\frac{2}{9}(h_{BC}^{M'} + h_{BD}^{M'} + h_{CD}^{M'})$			$\frac{3}{24}(h_{AB}^{M'} + h_{AC}^{M'} + h_{AD}^{M'} + h_{BC}^{M'} + h_{BD}^{M'} + h_{CD}^{M'})$		
Recom.	$\frac{1}{2}r_{AB}^{M'}$	$\frac{1}{2}r_{AC}^{M'}$	$\frac{1}{2}r_{AD}^{M'}$	$\frac{1}{2}r_{BC}^{M'}$	$\frac{2}{9}(r_{AB}^{M'} + r_{AC}^{M'} + r_{BC}^{M'})$	$\frac{2}{9}(r_{AB}^{M'} + r_{AD}^{M'} + r_{BD}^{M'})$
	$\frac{2}{9}(r_{BC}^{M'} + r_{BD}^{M'} + r_{CD}^{M'})$			$\frac{3}{24}(r_{AB}^{M'} + r_{AC}^{M'} + r_{AD}^{M'} + r_{BC}^{M'} + r_{BD}^{M'} + r_{CD}^{M'})$		

KEYNOTE ARTICLES

Table 6. Theoretical expectations for Terminal cross with three- and four-breed Backcross (BC₁) mating. (Note: Every shaded row is a continuation of the previous row to it)

Mating		Individual			Maternal		
Sire	Dam	Genetic	Heterosis	Recom.	Genetic	Heterosis	Recom.
		Paternal	Grandmaternal				
		Genetic	Genetic	Heterosis	Recom.		
Terminal cross with three-breed BC ₁ mating							
C	Ax(AxB)	$\frac{1}{2} g_C^I + \frac{1}{8} g_A^I + \frac{1}{8} g_B^I$	$\frac{3}{4} h_{CA}^I + \frac{1}{4} h_{CB}^I$	$\frac{1}{4} r_{AB}^I$	$\frac{3}{4} g_A^M + \frac{1}{4} g_B^M$	$\frac{1}{2} h_{AB}^M$	$\frac{1}{2} r_{AB}^M$
		g_C^P	$\frac{1}{2} (g_A^M + g_B^M)$	h_{AB}^M			
C	Bx(BxA)	$\frac{1}{2} g_C^I + \frac{1}{8} g_B^I + \frac{1}{8} g_A^I$	$\frac{3}{4} h_{CB}^I + \frac{1}{4} h_{CA}^I$	$\frac{1}{4} r_{BA}^I$	$\frac{3}{4} g_B^M + \frac{1}{4} g_A^M$	$\frac{1}{2} h_{BA}^M$	$\frac{1}{2} r_{BA}^M$
		g_C^P	$\frac{1}{2} (g_B^M + g_A^M)$	h_{BA}^M			
D	Ax(AxC)	$\frac{1}{2} g_D^I + \frac{1}{8} g_A^I + \frac{1}{8} g_C^I$	$\frac{3}{4} h_{DA}^I + \frac{1}{4} h_{DC}^I$	$\frac{1}{4} r_{AC}^I$	$\frac{3}{4} g_A^M + \frac{1}{4} g_C^M$	$\frac{1}{2} h_{AC}^M$	$\frac{1}{2} r_{AC}^M$
		g_D^P	$\frac{1}{2} (g_A^M + g_C^M)$	h_{AC}^M			
D	Cx(CxA)	$\frac{1}{2} g_D^I + \frac{1}{8} g_C^I + \frac{1}{8} g_A^I$	$\frac{3}{4} h_{DC}^I + \frac{1}{4} h_{DA}^I$	$\frac{1}{4} r_{CA}^I$	$\frac{3}{4} g_C^M + \frac{1}{4} g_A^M$	$\frac{1}{2} h_{CA}^M$	$\frac{1}{2} r_{CA}^M$
		g_D^P	$\frac{1}{2} (g_C^M + g_A^M)$	h_{CA}^M			
B	Ax(AxD)	$\frac{1}{2} g_B^I + \frac{1}{8} g_A^I + \frac{1}{8} g_D^I$	$\frac{3}{4} h_{BA}^I + \frac{1}{4} h_{BD}^I$	$\frac{1}{4} r_{AD}^I$	$\frac{3}{4} g_A^M + \frac{1}{4} g_D^M$	$\frac{1}{2} h_{AD}^M$	$\frac{1}{2} r_{AD}^M$
		g_B^P	$\frac{1}{2} (g_A^M + g_D^M)$	h_{AD}^M			
B	Dx(DxA)	$\frac{1}{2} g_B^I + \frac{1}{8} g_D^I + \frac{1}{8} g_A^I$	$\frac{3}{4} h_{BD}^I + \frac{1}{4} h_{BA}^I$	$\frac{1}{4} r_{DA}^I$	$\frac{3}{4} g_D^M + \frac{1}{4} g_A^M$	$\frac{1}{2} h_{DA}^M$	$\frac{1}{2} r_{DA}^M$
		g_B^P	$\frac{1}{2} (g_D^M + g_A^M)$	h_{DA}^M			
D	Bx(BxC)	$\frac{1}{2} g_D^I + \frac{1}{8} g_B^I + \frac{1}{8} g_C^I$	$\frac{3}{4} h_{DB}^I + \frac{1}{4} h_{DC}^I$	$\frac{1}{4} r_{BC}^I$	$\frac{3}{4} g_B^M + \frac{1}{4} g_C^M$	$\frac{1}{2} h_{BC}^M$	$\frac{1}{2} r_{BC}^M$
		g_D^P	$\frac{1}{2} (g_B^M + g_C^M)$	h_{BC}^M			
D	Cx(CxB)	$\frac{1}{2} g_D^I + \frac{1}{8} g_C^I + \frac{1}{8} g_B^I$	$\frac{3}{4} h_{DC}^I + \frac{1}{4} h_{DB}^I$	$\frac{1}{4} r_{CB}^I$	$\frac{3}{4} g_C^M + \frac{1}{4} g_B^M$	$\frac{1}{2} h_{CB}^M$	$\frac{1}{2} r_{CB}^M$
		g_D^P	$\frac{1}{2} (g_C^M + g_B^M)$	h_{CB}^M			
Terminal cross with four-breed BC ₁ mating							
D	Cx{Ax(AxB)}	$\frac{1}{2} g_D^I + \frac{1}{4} g_C^I + \frac{1}{16} g_A^I + \frac{1}{16} g_B^I$	$\frac{1}{2} h_{DC}^I + \frac{3}{8} h_{DA}^I + \frac{1}{8} h_{DB}^I$	$\frac{3}{8} r_{CA}^I + \frac{1}{8} r_{CB}^I$	$\frac{1}{2} g_C^M + \frac{3}{8} g_A^M + \frac{1}{8} g_B^M$	$\frac{3}{4} h_{CA}^M + \frac{1}{4} h_{CB}^M$	$\frac{1}{4} r_{AB}^M$
		g_D^P	$\frac{3}{4} g_A^M + \frac{1}{4} g_B^M$	$\frac{1}{2} h_{AB}^M$	$\frac{1}{2} r_{AB}^M$		
D	Cx{Bx(BxA)}	$\frac{1}{2} g_D^I + \frac{1}{4} g_C^I + \frac{1}{16} g_B^I + \frac{1}{16} g_A^I$	$\frac{1}{2} h_{DC}^I + \frac{3}{8} h_{DB}^I + \frac{1}{8} h_{DA}^I$	$\frac{3}{8} r_{CB}^I + \frac{1}{8} r_{CA}^I$	$\frac{1}{2} g_C^M + \frac{3}{8} g_B^M + \frac{1}{8} g_A^M$	$\frac{3}{4} h_{CB}^M + \frac{1}{4} h_{CA}^M$	$\frac{1}{4} r_{BA}^M$
		g_D^P	$\frac{3}{4} g_B^M + \frac{1}{4} g_A^M$	$\frac{1}{2} h_{BA}^M$	$\frac{1}{2} r_{BA}^M$		

3rd International Scientific Conference on Small Ruminant Development, Hurghada, Egypt, 12-15 April, 2010

B	Dx{Ax(AxC)}	$\frac{1}{2} g_B^I + \frac{1}{4} g_D^I + \frac{3}{16} g_A^I + \frac{1}{16} g_C^I$	$\frac{1}{2} h_{BD}^I + \frac{3}{8} h_{BA}^I + \frac{1}{8} h_{BC}^I$	$\frac{3}{8} r_{DA}^I + \frac{1}{8} r_{DC}^I$	$\frac{1}{2} g_D^M + \frac{3}{8} g_A^M + \frac{1}{8} g_C^M$	$\frac{3}{4} h_{DA}^M + \frac{1}{4} h_{DC}^M$	$\frac{1}{4} r_{AC}^M$
		g_B^P	$\frac{3}{4} g_A^M + \frac{1}{4} g_C^M$	$\frac{1}{2} h_{BC}^M$	$\frac{1}{2} r_{AC}^M$		
B	Dx{Cx(CxA)}	$\frac{1}{2} g_B^I + \frac{1}{4} g_D^I + \frac{3}{16} g_C^I + \frac{1}{16} g_A^I$	$\frac{1}{2} h_{BD}^I + \frac{3}{8} h_{BC}^I + \frac{1}{8} h_{BA}^I$	$\frac{3}{8} r_{DC}^I + \frac{1}{8} r_{DA}^I$	$\frac{1}{2} g_D^M + \frac{3}{8} g_C^M + \frac{1}{8} g_A^M$	$\frac{3}{4} h_{DC}^M + \frac{1}{4} h_{DA}^M$	$\frac{1}{4} r_{CA}^M$
		g_B^P	$\frac{3}{4} g_C^M + \frac{1}{4} g_A^M$	$\frac{1}{2} h_{CA}^M$	$\frac{1}{2} r_{CA}^M$		
C	Bx{Ax(AxD)}	$\frac{1}{2} g_C^I + \frac{1}{4} g_B^I + \frac{3}{16} g_A^I + \frac{1}{16} g_D^I$	$\frac{1}{2} h_{CB}^I + \frac{3}{8} h_{CA}^I + \frac{1}{8} h_{CD}^I$	$\frac{3}{8} r_{BA}^I + \frac{1}{8} r_{BD}^I$	$\frac{1}{2} g_B^M + \frac{3}{8} g_A^M + \frac{1}{8} g_D^M$	$\frac{3}{4} h_{BA}^M + \frac{1}{4} h_{BD}^M$	$\frac{1}{4} r_{AD}^M$
		g_C^P	$\frac{3}{4} g_A^M + \frac{1}{4} g_D^M$	$\frac{1}{2} h_{AD}^M$	$\frac{1}{2} r_{AD}^M$		
C	Bx{Dx(DxA)}	$\frac{1}{2} g_C^I + \frac{1}{4} g_B^I + \frac{3}{16} g_D^I + \frac{1}{16} g_A^I$	$\frac{1}{2} h_{CB}^I + \frac{3}{8} h_{CD}^I + \frac{1}{8} h_{CA}^I$	$\frac{3}{8} r_{BD}^I + \frac{1}{8} r_{BA}^I$	$\frac{1}{2} g_B^M + \frac{3}{8} g_D^M + \frac{1}{8} g_A^M$	$\frac{3}{4} h_{BD}^M + \frac{1}{4} h_{BA}^M$	$\frac{1}{4} r_{DA}^M$
		g_C^P	$\frac{3}{4} g_D^M + \frac{1}{4} g_A^M$	$\frac{1}{2} h_{DA}^M$	$\frac{1}{2} r_{DA}^M$		
A	Dx{Bx(BxC)}	$\frac{1}{2} g_A^I + \frac{1}{4} g_D^I + \frac{3}{16} g_B^I + \frac{1}{16} g_C^I$	$\frac{1}{2} h_{AD}^I + \frac{3}{8} h_{AB}^I + \frac{1}{8} h_{AC}^I$	$\frac{3}{8} r_{DB}^I + \frac{1}{8} r_{DC}^I$	$\frac{1}{2} g_D^M + \frac{3}{8} g_B^M + \frac{1}{8} g_C^M$	$\frac{3}{4} h_{DB}^M + \frac{1}{4} h_{DC}^M$	$\frac{1}{4} r_{BC}^M$
		g_A^P	$\frac{3}{4} g_B^M + \frac{1}{4} g_C^M$	$\frac{1}{2} h_{BC}^M$	$\frac{1}{2} r_{BC}^M$		
A	Dx{Cx(CxB)}	$\frac{1}{2} g_A^I + \frac{1}{4} g_D^I + \frac{3}{16} g_C^I + \frac{1}{16} g_B^I$	$\frac{1}{2} h_{AD}^I + \frac{3}{8} h_{AC}^I + \frac{1}{8} h_{AB}^I$	$\frac{3}{8} r_{DC}^I + \frac{1}{8} r_{DB}^I$	$\frac{1}{2} g_D^M + \frac{3}{8} g_C^M + \frac{1}{8} g_B^M$	$\frac{3}{4} h_{DC}^M + \frac{1}{4} h_{DB}^M$	$\frac{1}{4} r_{CB}^M$
		g_A^P	$\frac{3}{4} g_C^M + \frac{1}{4} g_B^M$	$\frac{1}{2} h_{CB}^M$	$\frac{1}{2} r_{CB}^M$		

KEYNOTE ARTICLES

Table 7. Theoretical expectations for Terminal cross with two-, three- and four-breed Rotational cross mating (with equal proportion of breeds). (Note: Every shaded raw is a continuation of the previous raw to it)

Effects	Two-breed Rotation				Three-breed Rotation
	Cx[A-B]	Bx[A-C]	Bx[A-D]	Ax[B-C]	Cx[A-B-D]
	Three-breed Rotation		Four-breed Rotation		
	Ax[B-C-D]		Cx[A-B-C-D]		
Individual					
Genetic	$\frac{1}{2} g'_c + \frac{1}{4} (g'_a + g'_b)$	$\frac{1}{2} g'_b + \frac{1}{4} (g'_a + g'_c)$	$\frac{1}{2} g'_a + \frac{1}{4} (g'_b + g'_c)$	$\frac{1}{2} g'_a + \frac{1}{4} (g'_b + g'_c)$	$\frac{1}{2} g'_c + \frac{1}{6} (g'_a + g'_b + g'_d)$
	$\frac{1}{2} g'_a + \frac{1}{6} (g'_b + g'_c + g'_d)$		$\frac{1}{2} g'_b + \frac{1}{6} (g'_a + g'_c + g'_d)$		
Heterosis	$\frac{1}{2} (h'_{ca} + h'_{cb})$	$\frac{1}{2} (h'_{ba} + h'_{bc})$	$\frac{1}{2} (h'_{ca} + h'_{cb})$	$\frac{1}{2} (h'_{ab} + h'_{ac})$	$\frac{1}{3} (h'_{ca} + h'_{cb} + h'_{cd})$
	$\frac{1}{2} (h'_{ab} + h'_{ac} + h'_{ad})$		$\frac{1}{2} (h'_{ba} + h'_{bc} + h'_{bd})$		
Recom.	$\frac{2}{3} r'_{bc}$	$\frac{2}{3} r'_{ac}$	$\frac{2}{3} r'_{ca}$	$\frac{2}{3} r'_{bc}$	$\frac{6}{63} (r'_{ab} + r'_{cd} + r'_{bd})$
	$\frac{2}{63} (r'_{bc} + r'_{bd} + r'_{cd})$		$\frac{2}{270} (r'_{ab} + r'_{ac} + r'_{ad} + r'_{bc} + r'_{bd} + r'_{cd})$		
Maternal					
Genetic	$\frac{1}{2} (g^M_c + g^M_b)$	$\frac{1}{2} (g^M_b + g^M_c)$	$\frac{1}{2} (g^M_a + g^M_b)$	$\frac{1}{2} (g^M_b + g^M_c)$	$\frac{1}{3} (g^M_a + g^M_b + g^M_d)$
	$\frac{1}{3} (g^M_b + g^M_c + g^M_d)$		$\frac{1}{3} (g^M_a + g^M_b + g^M_c + g^M_d)$		
Heterosis	$\frac{2}{3} h^M_{bc}$	$\frac{2}{3} h^M_{ac}$	$\frac{2}{3} h^M_{ca}$	$\frac{2}{3} h^M_{bc}$	$\frac{6}{21} (h^M_{ab} + h^M_{ad} + h^M_{bd})$
	$\frac{6}{21} (h^M_{bc} + h^M_{bd} + h^M_{cd})$		$\frac{6}{96} (h^M_{ab} + h^M_{ac} + h^M_{ad} + h^M_{bc} + h^M_{bd} + h^M_{cd})$		
Recom.	$\frac{1}{21} r^M_{bc}$	$\frac{1}{21} r^M_{ac}$	$\frac{1}{21} r^M_{ca}$	$\frac{1}{21} r^M_{bc}$	$\frac{1}{21} (r^M_{ab} + r^M_{ad} + r^M_{bd})$
	$\frac{1}{21} (r^M_{bc} + r^M_{bd} + r^M_{cd})$		$\frac{1}{96} (r^M_{ab} + r^M_{ac} + r^M_{ad} + r^M_{bc} + r^M_{bd} + r^M_{cd})$		
Paternal					
Genetic	g^P_c	g^P_b	g^P_a	g^P_a	g^P_c
	g^P_a		g^P_b		
Grand-maternal					
Genetic	$\frac{1}{2} (g^M_c + g^M_b)$	$\frac{1}{2} (g^M_b + g^M_c)$	$\frac{1}{2} (g^M_a + g^M_b)$	$\frac{1}{2} (g^M_b + g^M_c)$	$\frac{1}{3} (g^M_a + g^M_b + g^M_d)$
	$\frac{1}{3} (g^M_b + g^M_c + g^M_d)$		$\frac{1}{3} (g^M_a + g^M_b + g^M_c + g^M_d)$		
Heterosis	$\frac{2}{3} h^M_{bc}$	$\frac{2}{3} h^M_{ac}$	$\frac{2}{3} h^M_{ca}$	$\frac{2}{3} h^M_{bc}$	$\frac{6}{21} (h^M_{ab} + h^M_{ad} + h^M_{bd})$
	$\frac{6}{21} (h^M_{bc} + h^M_{bd} + h^M_{cd})$		$\frac{6}{96} (h^M_{ab} + h^M_{ac} + h^M_{ad} + h^M_{bc} + h^M_{bd} + h^M_{cd})$		
Recom.	$\frac{1}{21} r^M_{bc}$	$\frac{1}{21} r^M_{ac}$	$\frac{1}{21} r^M_{ca}$	$\frac{1}{21} r^M_{bc}$	$\frac{1}{21} (r^M_{ab} + r^M_{ad} + r^M_{bd})$
	$\frac{1}{21} (r^M_{bc} + r^M_{bd} + r^M_{cd})$		$\frac{1}{96} (r^M_{ab} + r^M_{ac} + r^M_{ad} + r^M_{bc} + r^M_{bd} + r^M_{cd})$		

Table 8. Theoretical expectations for Terminal cross with Two-, Three- and Four breed Synthetic population (with equal proportion of breeds).

Effects	Two-breed Synthetic				Three-breed Synthetic
	Cx[A:B]	Bx[A:C]	Bx[A:D]	Ax[B:C]	Cx[A:B:D]
	Three-breed Synthetic		Four-breed Synthetic		
	Ax[B:C:D]	Zx[A:B:C:D]			
Individual					
Genetic	$\frac{1}{2} g'_C + \frac{1}{4} (g'_A + g'_B)$	$\frac{1}{2} g'_B + \frac{1}{4} (g'_A + g'_C)$	$\frac{1}{2} g'_B + \frac{1}{4} (g'_A + g'_D)$	$\frac{1}{2} g'_A + \frac{1}{4} (g'_B + g'_C)$	$\frac{1}{2} g'_C + \frac{1}{6} (g'_A + g'_B + g'_D)$
Heterosis	$\frac{1}{2} (h'_{CA} + h'_{CB})$	$\frac{1}{2} (h'_{BA} + h'_{BC})$	$\frac{1}{2} (h'_{BA} + h'_{BD})$	$\frac{1}{2} (h'_{AB} + h'_{AC})$	$\frac{1}{3} (h'_{CA} + h'_{CB} + h'_{CD})$
Recom.	$\frac{1}{2} r'_{AB}$	$\frac{1}{2} r'_{AC}$	$\frac{1}{2} r'_{AD}$	$\frac{1}{2} r'_{BC}$	$\frac{2}{9} (r'_{AB} + r'_{AD} + r'_{BD})$
Maternal					
Genetic	$\frac{1}{2} (g^M_A + g^M_B)$	$\frac{1}{2} (g^M_A + g^M_C)$	$\frac{1}{2} (g^M_A + g^M_D)$	$\frac{1}{2} (g^M_B + g^M_C)$	$\frac{1}{3} (g^M_A + g^M_B + g^M_D)$
Heterosis	$\frac{1}{2} h^M_{AB}$	$\frac{1}{2} h^M_{AC}$	$\frac{1}{2} h^M_{AD}$	$\frac{1}{2} h^M_{BC}$	$\frac{2}{9} (h^M_{AB} + h^M_{AD} + h^M_{BD})$
Recom.	$\frac{1}{2} r^M_{AB}$	$\frac{1}{2} r^M_{AC}$	$\frac{1}{2} r^M_{AD}$	$\frac{1}{2} r^M_{BC}$	$\frac{2}{9} (r^M_{AB} + r^M_{AD} + r^M_{BD})$
Paternal					
Genetic	g^P_C	g^P_B	g^P_B	g^P_A	g^P_C
Grand-maternal					
Genetic	$\frac{1}{2} (g^{M'}_A + g^{M'}_B)$	$\frac{1}{2} (g^{M'}_A + g^{M'}_C)$	$\frac{1}{2} (g^{M'}_A + g^{M'}_D)$	$\frac{1}{2} (g^{M'}_B + g^{M'}_C)$	$\frac{1}{3} (g^{M'}_A + g^{M'}_B + g^{M'}_D)$
Heterosis	$\frac{1}{2} h^{M'}_{AB}$	$\frac{1}{2} h^{M'}_{AC}$	$\frac{1}{2} h^{M'}_{AD}$	$\frac{1}{2} h^{M'}_{BC}$	$\frac{2}{9} (h^{M'}_{AB} + h^{M'}_{AD} + h^{M'}_{BD})$
Recom.	$\frac{1}{2} r^{M'}_{AB}$	$\frac{1}{2} r^{M'}_{AC}$	$\frac{1}{2} r^{M'}_{AD}$	$\frac{1}{2} r^{M'}_{BC}$	$\frac{2}{9} (r^{M'}_{AB} + r^{M'}_{AD} + r^{M'}_{BD})$

KEYNOTE ARTICLES

Table 9. Estimates of individual heterosis (h^I), maternal heterosis (h^M) and paternal heterosis (h^P) effects in sheep presented by reference and breed population.

	Body weight (kg) at			Daily gain (g)		Fert.	Prolif.	Fec.	Lamb surv. %	Grease fleece		Wean	Market
	Birth	Wean (d)	Yearling (d)	Pre-wean	Post-wean					Weight	Grade		
Miller and Dailey (1951)													
				Columbia, Hampshire and Shropshire									
h^I	0.23	1.4 (140d)	•	•	•	•	0.05	0.17	•	0.32	0.21	4.5 ^a	•
%	6	4	•	•	•	•	3	15	•	7	6	19	•
Sidwell et al. (1962, 1964)													
				Hampshire, Shropshire, Southdown, Merino and Columbia-Southdown									
h^I	0.21	2.3 (120d)	•	17	•	•	2.0	10.3	14.0 ^b	3.6	•	•	•
%	6.1	9.8	•	10.1	•	•	2.3	7.5	15.6	4.5	•	•	•
h^M	0.30	3.9 (120d)	•	29	•	•	•	•	•	•	•	•	•
%	8.9	16.6	•	17.8	•	•	•	•	•	•	•	•	•
Donald et al. (1963)													
				Scottish Blackface and Swaledale									
h^I	0.09	0.82 (105d)	•	•	•	•	•	4.2	•	0.11	•	0.8	•
%	2.6	2.9	•	•	•	•	•	3.4	•	5.1	•	2.7	•
Botkin and Paules (1965)													
				Corriedale and Suffolk									
h^I	•	1.1 (180d)	•	•	•	•	•	22.9 ^b	•	0.35	•	(9.6)	•
%	•	3.1	•	•	•	•	•	27.5	•	10.9	•	(32.1)	•
Lal et al. (1966)													
				Columbia and Targhee									
h^I	0.14	0.27 (30d)	0.59 (90d)	5	8	•	•	•	•	•	•	•	•
%	3	2.4	2.2	2	2.2	•	•	•	•	•	•	•	•
Singh et al. (1967)													
				Minnesota									
h^I	0.21	2.19 (100d)	•	•	•	•	•	•	•	•	•	•	•
%	4.7	8.1	•	•	•	•	•	•	•	•	•	•	•
McGuirk (1967)													
				Merino and Border Leicester									
h^I	0.16	1.91	•	16	•	•	17.8	46	47	•	0.45	•	•
%	3.5	6.5	•	7.1	•	•	24.9	44	49	•	9.6	•	•
Holtzman and Bernard (1969)													
				Oxford, Suffolk and N.C. Cheviot									
h^I	0.18	1.16 (28d)	0.22 (120d)	•	27	•	•	•	•	•	•	•	•
%	4.6	10.2	0.7	•	13	•	•	•	•	•	•	•	•
h^M	0.41	1.9 (28d)	3.3 (120d)	•	25	•	•	•	•	•	•	•	•
%	9.9	16.9	11.2	•	12	•	•	•	•	•	•	•	•
Ercanbrack et al. (1970)													
				Targhee and Columbia									
h^I	•	1.04	•	•	•	•	•	•	•	•	•	•	•

3rd International Scientific Conference on Small Ruminant Development, Hurghada, Egypt, 12-15 April, 2010

Iwan et al. (1971)			Merino and Corriedale										
h^I	0.04	.	0.09	2.6	.
%	3.6	.	9.7	10.7	.
Sidwell and Miller (1971a,b,c)			Hampshire, Targhee, Suffolk, Dorset and Columbia-Southdown										
h^I	0.11	1.3 (85d)	.	15	.	3.9	5.2	9.2	7.5	.	.	(6.76)	.
%	2.4	5	.	6.1	.	5.7	3.3	10.8	9.3	.	.	(23.4)	.
Bradley et al. (1972)			Suffolk, Targhee and Shropshire										
h^I	.	0.9 (120d)	0.3	-0.1 ^b	2.2	.	.	(0.5)	.
%	.	2.8	1.9	-0.8	16.7	.	.	(1)	.
Ryder and Wilson (1972)			Finnsheep and Merino										
h^I	-2.4	.
%	-0.18	.
Carter and Copenhaver (1972)^c			Dorset and Rambouillet										
h^I	-0.25	-7	.	0.24	.	7.5	.	.	.
%	-5.5	-2.8	.	15.4	.	27.3	.	.	.
Vesely and Peters (1972, 1974)			Romnelet, Columbia, Suffolk and N.C. Cheviot										
h^I	.	1.2 (108d)	3.0 (183d)	.	17	2.2	5.3	21.0 ^b	11 ^b	.	.	3.7 (3.8)	7.0 (6.0)
%	.	4.8	7.3	.	7.5	2.7	3.9	25.2	14.3	.	.	11.4 (16.8)	13.5 (16.6)
h^M	.	3.5 (108d)	4.7 (183d)	.	16	8.2 (8.2)	12.1 (11.8)
%	.	14.6	11.4	.	6.9	25.2 (36.3)	23.3 (32.6)
Galal et al. (1972)			German Mutton Merino, Ossimi and Barki										
h^I	0.06	0.49 (120d)	1.95	0.06	0.32	.	.	.
%	2.1	3	6.8	7.3	31.5	.	.	.
Aboul-Naga and Galal (1973)			German Mutton Merino, Ossimi and Barki										
h^I	0.24	0.10 (120d)	1.62	-0.04	0.4	.	.	.
h^M	0.60 ^a	2.14 (120d)	2.00	-0.02	0.17	.	.	.
Fahmy and Bernard (1973)			Oxford and Suffolk										
h^I	9.6 ^d	.	.	0.48	.	.	.
%	22.9	.	.	17.1	.	.	.
h^M	22.3
%	53
Land et al. (1974)			Finnsheep and Tasmanian Merino										
h^I	0.10	-14	6 ^b
%	12.9	-7.6	3.8
Peters and Heaney (1974)			Suffolk and Shropshire										
h^I	0.3	1.1 (70d)	2.4 (140d)	12	28
%	7.5	6.5	8.4	6.5	10.4

KEYNOTE ARTICLES

Wiener and Hayter (1974)	Scottish Blackface, N.C. Cheviot, Welsh Mountain and Lincoln
h^1	.
%	. -0.38 (42d) 2.9 (126d)
Wiener and Hayter (1975)	Scottish Blackface, N.C. Cheviot and Welsh Mountain
h^1 0.01 0.11 0.1 3.2 . .
% 1.4 7.7 12.6 8.4 . .
Dickerson et al. (1975)	Hampshire, Dorset, Rambouillet and Coarse Wool
h^1	.
% 0.5 (70d) 0.34 5.9
Dickerson et al. (1975)	Fleischsheep and Domestic sheep in USA
% 0.9 (70d) 0.7 8.8
More O'Ferrall (1975)^c	Galway and Scottish Blackface
h^1 10.2 0.09 0.2 2 0.3 4.05 (6.3) . .
% 13 6 21 10 11 13 (24) . .
More O'Ferrall (1975)^c	Galway and Wicklow Cheviot
h^1 3.8 -0.08 0 1.5 0 0.25 (1.1) . .
% 5 -5 0 7 1 1 (4) . .
More O'Ferrall (1975)^c	Border Leicester and Scottish Blackface
h^1 7.7 0.14 0.19 -2 0.6 3 (5.3) . .
% 9 9 18 -11 27 8 (18) . .
More O'Ferrall (1975)^c	Border Leicester and Wicklow Cheviot
h^1 2 -0.02 0.01 -2.7 0.3 -0.7 (0.2) . .
% 2 -1 1 -14 11 -2 (1) . .
Rastogi et al. (1975)	Columbia, Suffolk and Targhee
h^1	0.08 0.38 (70d) 6 12 (70-133d)
%	1.6 1.5 2.1 4.3
Hohenboken and Cochran (1976)	Hampshire, Suffolk and Willamette
h^1 10 0.15 -9.3 4.1 (4.2)
% 18 14.1 -11.2 13.5 (29.8)
Hohenboken et al. (1976a, b)	Hampshire, Suffolk and Willamette
h^1	.
%	1.2 5.6 (136d) 5.7 1.8 3.2 8.6 (13.5)
Vesely et al. (1977)	Romnelet, Columbia, Suffolk and N.C. Cheviot
h^1	0.12 1.3 (108d) 2.5 (183d) 14 6
%	2.6 5.3 6.1 7.2 10.3
Vesely and Peters (1972, 1974)	Romnelet, Columbia, Suffolk and N.C. Cheviot
h^1 1.2 (110d) 2.6 (185d) 20
% 5 6 6

3rd International Scientific Conference on Small Ruminant Development, Hurghada, Egypt, 12-15 April, 2010

Sierra (1980, 1982)		Aragonesa and Romanov									
h^1
%
Ollenacu and Boylan (1981a,b)^f		Finnsheep, Minnesota 100, Suffolk and Targhee									
h^1	-0.01	0.33 (70d)	(3.99)
%	-4	1.9	(22.5)
Rastogi et al. (1982)		Columbia, Suffolk and Targhee									
h^1	0.22	0.13 (70d)	.	-2.3	-0.3 (70-133d)
%	4.6	0.7	.	-0.6	-0.2
h^M	0.03	-0.08 (70d)	.	-2.2	-14 (70-133d)
%	0.7	-0.2	.	-0.7	-4.6
Ch'ang and Evans (1982)		Dorset, Merino and Corriedale									
h^1	.	(84-91d)	(0.74)
%	(7.6)
h^M	.	(84-91d)	(3.82)
%	(39)
h^F	.	(84-91d)	(2.35)
%	(24)
Shrestha et al. (1983)		Minnesota									
h^M	.	.	.	-16.6	2.2	-10	5.2	.	.	1.62	7.64
%	.	.	.	-16.8	1.6	-8.5	6	.	.	28.1	23
Fogarty et al. (1984)^e		Finnsheep, Rambouillet and Dorset (Composite 1)									
h^1	-0.45 (-3.53)
%	-3.7 (-37.7)
Fogarty et al. (1984)^e		Finnsheep, Suffolk and Targhee (Composite 2)									
h^1	-0.25 (-4.25)
%	-2 (-51)
Iniguez et al. (1986)		Dorset and Finnsheep									
h^1	.	.	.	2.2	-0.04	0.05	(0.65)
%	.	.	.	2.4	-2.4	4.2	(3.1)
Ch'ang and Evans (1986)		Dorset, Merino and Corriedale									
h^P	.	-0.3 (88d)	(1.6)
%	.	-1.5	(6.6)
Tchamitchian et al (1986)		Romanov and Berrichon du Cher									
h^1	1.3
Long et al. (1989)		Suffolk and Targhee									
h^1	.	0.77 (90d)	0.55	0.05	.	5.39	3.88

KEYNOTE ARTICLES

%	•	2.8	•	•	•	0.64	3.3	•	6.9	•	•	13.8	•
h^M	•	1.47 (90d)	•	•	•	2.3	0.1	•	1.14	•	•	2.99	•
%	•	5.4	•	•	•	2.6	6.6	•	1.4	•	•	10.1	•
Boujenane and Bradford (1991)				D'man and Sardi									
h^I	•	1.08 (60d)	•	•	•	0.15	0.05	0.05	•	•	•	(3.22)	•
%	•	9.4	•	•	•	18.9	3.5	4.1	•	•	•	30.5	•
h^M	•	0.03 (60d)	•	•	•	-0.02	0.05	0.05	•	•	•	(0.46)	•
%	•	0.3	•	•	•	-2.15	3.5	4.1	•	•	•	4.4	•
Boujenane et al (1991a,b)				D'man and Sardi									
h^I	-0.03	0.29 (90d)	1.49	•	•	•	-0.03	•	-0.02	•	•	•	•
%	-1.1	2.1	5.2	•	•	•	-2	•	-2.1	•	•	•	•
h^M	-0.05	0.25 (90d)	-0.32	•	•	•	0.06	•	-0.001	•	•	•	•
%	-1.8	1.8	-1.1	•	•	•	4	•	-0.1	•	•	•	•
Fahmy (1996b)				DLS, Finnsheep and Romanov									
h^I	-0.07	0.78 (50d)	•	•	•	•	•	•	•	•	•	•	•
%	-2.2	5.9	•	•	•	•	•	•	•	•	•	•	•
Boujenane and Kansari (2002)^f				D'man and Lacaune									
h^I	-0.5	-0.84 (30d)	-1.35 (70d)	•	•	•	0.1	0.15	0.04	•	•	•	0.9
%	-14.9	-9.5	-8.2	•	•	•	6.2	11.6	5.1	•	•	•	4.1
h^M	-0.03	0.55 (30d)	0.25 (70d)	•	•	•	-0.17	-0.08	0.03	•	•	•	0.1
%	-0.9	6.2	1.5	•	•	•	-10.6	-6.2	3.8	•	•	•	0.5
Malik and Singh (2006)^g				Corriedale, Russian Merino and Nali									
h^I	•	•	•	•	•	•	•	•	•	0.004	•	•	•
h^M	•	•	•	•	•	•	•	•	•	0.029	•	•	•
Shrestha et al. (2008a,b)				Finnsheep and Romanov									
h^I	0.18	0.8 (30d)	4 (140d)	23	25	•	0.15	18.5	6.9	0.2	-1.4	4	20.9
%	6	8.9	10	11.4	11.1	•	4.9	8.2	9.9	9.5	-25.7	22	27
Shrestha et al. (2008a,b)				Outaouais and Rideau									
h^I	0.16	0.7 (30d)	3.7 (140d)	21	22	•	0.15	0.5	-1.3	0.5	0	1.7	20.8
%	4.5	6.8	8.3	9.4	8.7	•	5.4	0.2	-1.6	21.7	0	8.4	27.8

Fertility = number of ewes lambing per ewe exposed, %; Prolificacy = number of lambs born alive per ewe lambing; Fecundity = number of lambs weaned per ewe lambing (per ewe bred), %; Lamb survival = lambs weaned of live lambs born, %.

^a Lambs wt. per 45.4 kg ewe weight.

^b Lambs weaned or raised per ewe bred.

^c Estimated from purebreds and single cross (no reciprocal cross).

^d multiple birth.

^e Estimates from purebred and Finnsheep sired single cross.

^f Estimated from one purebred, F1, F2 and their reciprocal crossbreds.

^g Estimated from interbreeding among backcrosses.

Table 10. Estimates of recombination (r^1) and heterosis retention (h^{F1-F2}) effects in sheep presented by reference and breed population.

	Body weight (kg) at			Daily gain (g)		Fert.	Prolif.	Fec.	Lamb surv. %	Grease fleece					
	Lamb wt./ewe lambing (exposed)			Pre-wean	Post-wean					%	%	Weight	Grade	Wean	Market
	Birth	Wean (d)	Yearling (d)												
Peters et al. (1961)	Romnelet														
h^{F1-F2}	-0.59	-3.4 (100-116d)	-3.18 (18mo)	*	*	*	*	*	*	-0.27 ^a	*	*			
Pattie and Smith (1964)	Border Leicester and Merino														
h^{F1-F2}	*	-0.09 (18mo)	*	*	-5.6	-37	*	-19.2	-0.14	*	*	*			
%	*	-0.3	*	*	-6	-21	*	-24	-4	*	*	*			
Hight and Jury (1970a,b; 1971)	Border Leicester and Romney														
h^{F1-F2}	-0.05	0.14	-1.7	*	-4.7	-11	-14	-4.3	0.06	*	*	*			
%	1	1	-4	*	-5	-9	-13	-5	7	*	*	*			
Vesely and Peters (1979)	Romnelet														
h^{F1-F2}	-0.1 (110d)	0.2 (185d)	*	2	*	*	*	*	*	*	*	*			
%	-0.4	0.4	*	1	*	*	*	*	*	*	*	*			
Oftencu and Boylan (1981a,b)	Flinnsheep, Minnesota 100, Suffolk and Targhee														
h^{F1-F2}	-0.15	0.2 (70d)	*	*	*	-12	-18	4.9	-0.4	*	(-4.3)	*			
%	-5	1	*	*	*	-7	-13	6	-15	*	(-15)	*			
Rastogi et al. (1982)	Columbia, Suffolk and Targhee														
$\frac{1}{2}r^1$	0.07	1.13 (70d)	*	16	13.5 (70-133d)	*	*	*	*	*	*	*			
%	1.4	4.6	*	5.7	4.4	*	*	*	*	*	*	*			
Fogarty et al. (1984)^b	Flinnsheep, Rambouillet and Dorset (Composite 1)														
h^k	*	*	*	*	13.6	0.07	36	10.3	*	*	0.1 (4)	*			
%	*	*	*	*	19.8	3.4	44.4	14.9	*	*	0.9 (43)	*			
Fogarty et al. (1984)^b	Flinnsheep, Suffolk and Targhee (Composite 2)														
h^k	*	*	*	*	11.4	-0.05	28	10.9	*	*	0.1 (3.2)	*			
%	*	*	*	*	16.6	-2.4	34.6	15.7	*	*	0.9 (34.4)	*			
Ch'ang and Evans (1986)	Dorset, Merino and Corriedale														
r^1	*	0 (84-91d)	*	*	-2.1	-0.11	0.2	*	*	*	(-1.1)	*			
%	*	0	*	*	-2.3	-7.4	0.3	*	*	*	(-4.5)	*			
Boujenane and Bradford (1991)	D'man and Sardi														
r^1	*	-0.17	*	*	0.04	-0.04	-0.07	*	*	*	(-1.00)	*			
%	*	-1.5	*	*	5	-2.8	-5.7	*	*	*	(-9.5)	*			

KEYNOTE ARTICLES

Boujenane et al (1991a,b)			D'man and Sardi										
r^1	-0.11	-1.11	0.03	•	•	•	-0.01	-0.06	•	•	•	•	
%	-3.9	-8	0.1	•	•	•	-0.7	-6.3	•	•	•	•	
Shrestha et al. (2008a,b)			Synthetic I										
h^R	0.14	1.4 (30d)	8.6 (140d)	43	52	•	0.3	38	12.6	-0.7	0.2	5.0	20.2
%	3.8	15.1	21.5	22.2	23.7	•	13.6	25	19	-15.9	3.8	32.9	31.9
Shrestha et al. (2008a,b)			Synthetic II										
h^R	0.28	0.35 (30d)	3.3 (140d)	2	21	•	0.3	33	6.6	-0.35	0.15	1.9	11.8
%	7	3.3	7.6	0.7	8.9	•	18.8	26.5	8.3	-8.2	5.3	11.8	19.5
Shrestha et al. (2008a,b)			Synthetic III										
h^R	0.05	1.23 (30d)	6.28 (140d)	40	38	•	0.4	56	13.9	-0.5	0.23	5.2	22.9
%	1.2	12.3	15.1	19.3	16.7	•	21.1	40.6	19.1	-12.1	5.5	33.5	36.9

Fertility = number of ewes lambing per ewe exposed, %; Prolificacy = number of lambs born alive per ewe lambing; Fecundity = number of lambs weaned per ewe lambing (per ewe bred), %; Lamb survival = lambs weaned of live lambs born, %.

h^R = Composite population – parental purebreds.

^a clean fleece.

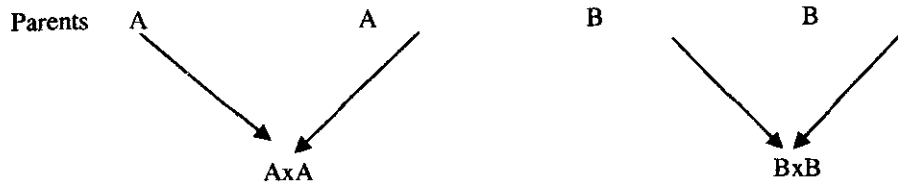
^b

multiple

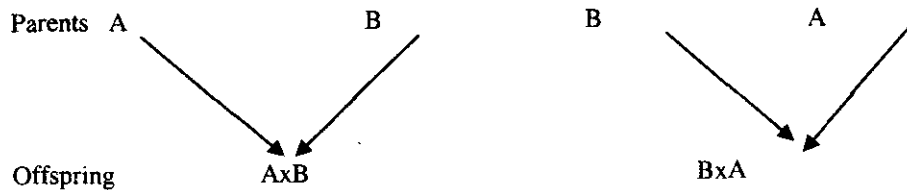
birth.

Figure 1. Purebred, Single-cross (F1), F2 and F3 mating.

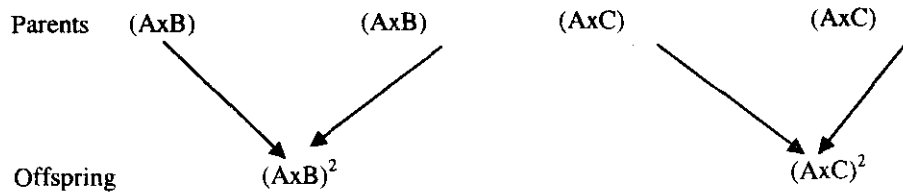
Purebreed



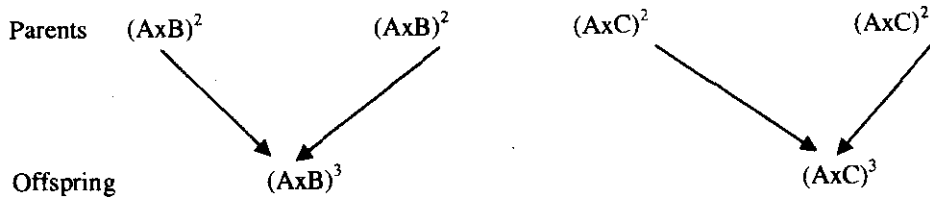
Single cross (F1)



F2



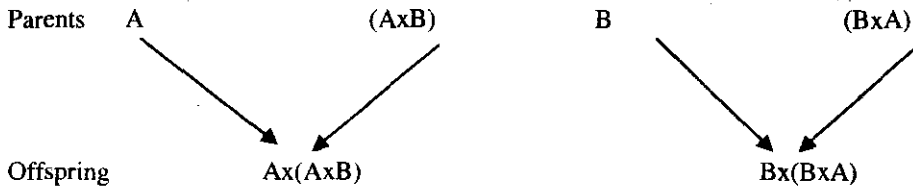
F3



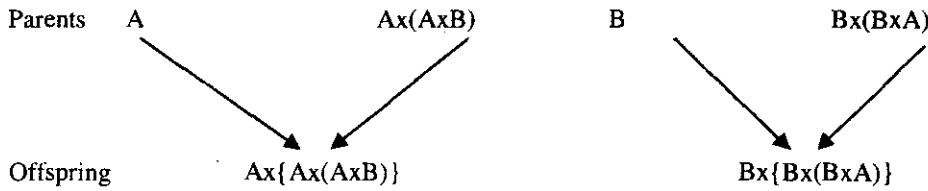
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Figure 2. Back-cross (BC1, BC2 and BC3) mating.

Backcross (BC1)



Backcross (BC2)



Backcross (BC3)

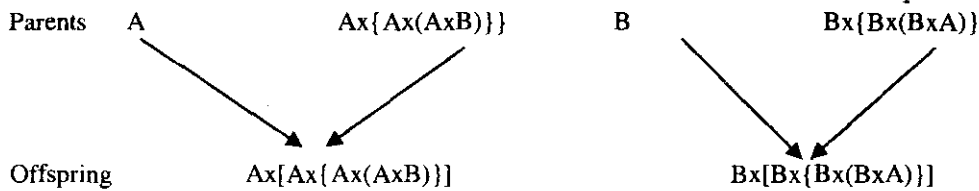
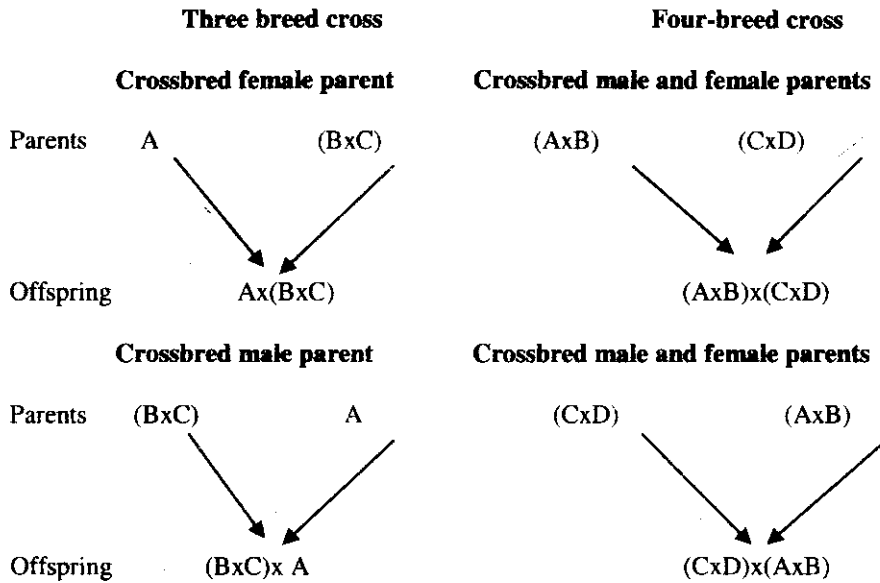


Figure 3. Specific three- and four-breed cross mating.



GENETIC & BREEDING

Figure 4. Two-, three- and four-breed Rotational cross mating (with equal proportion of breeds).

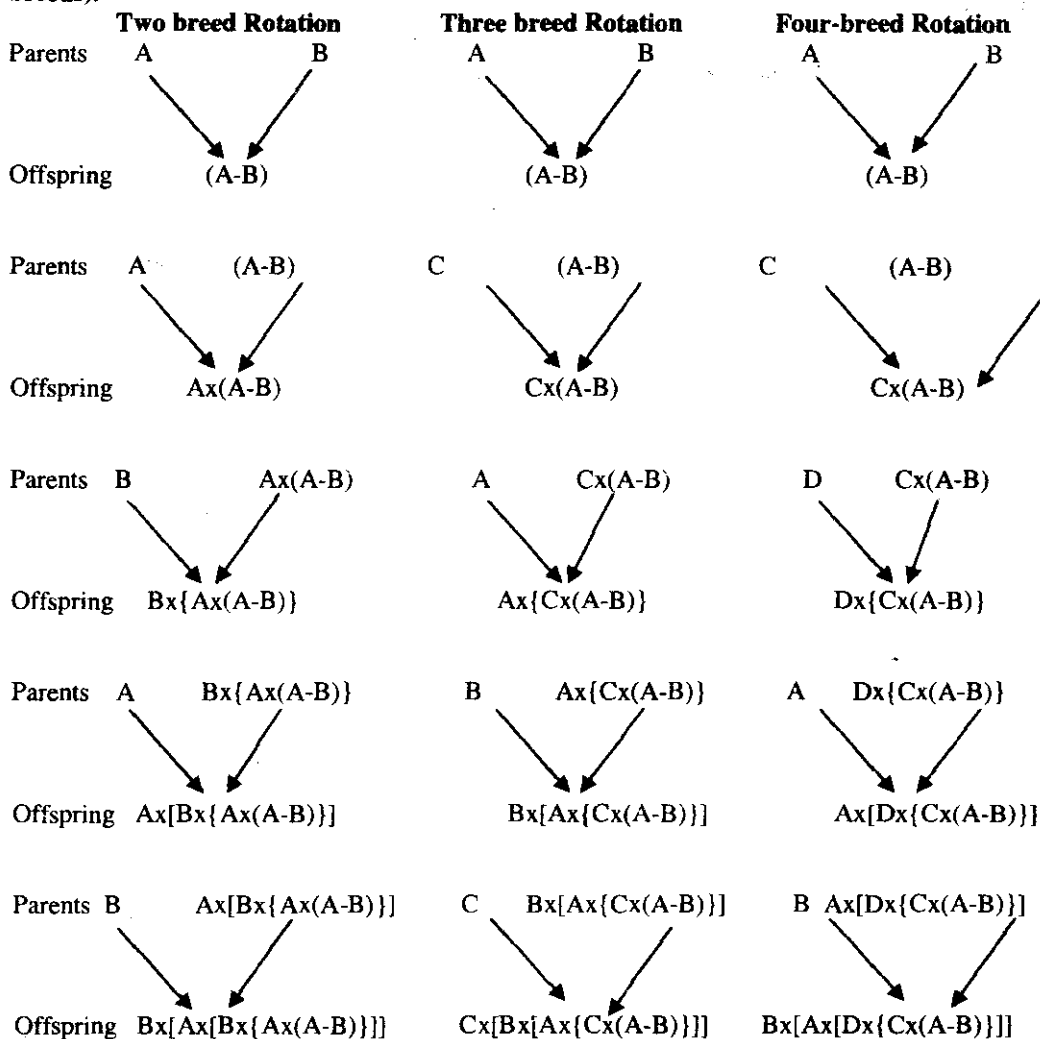
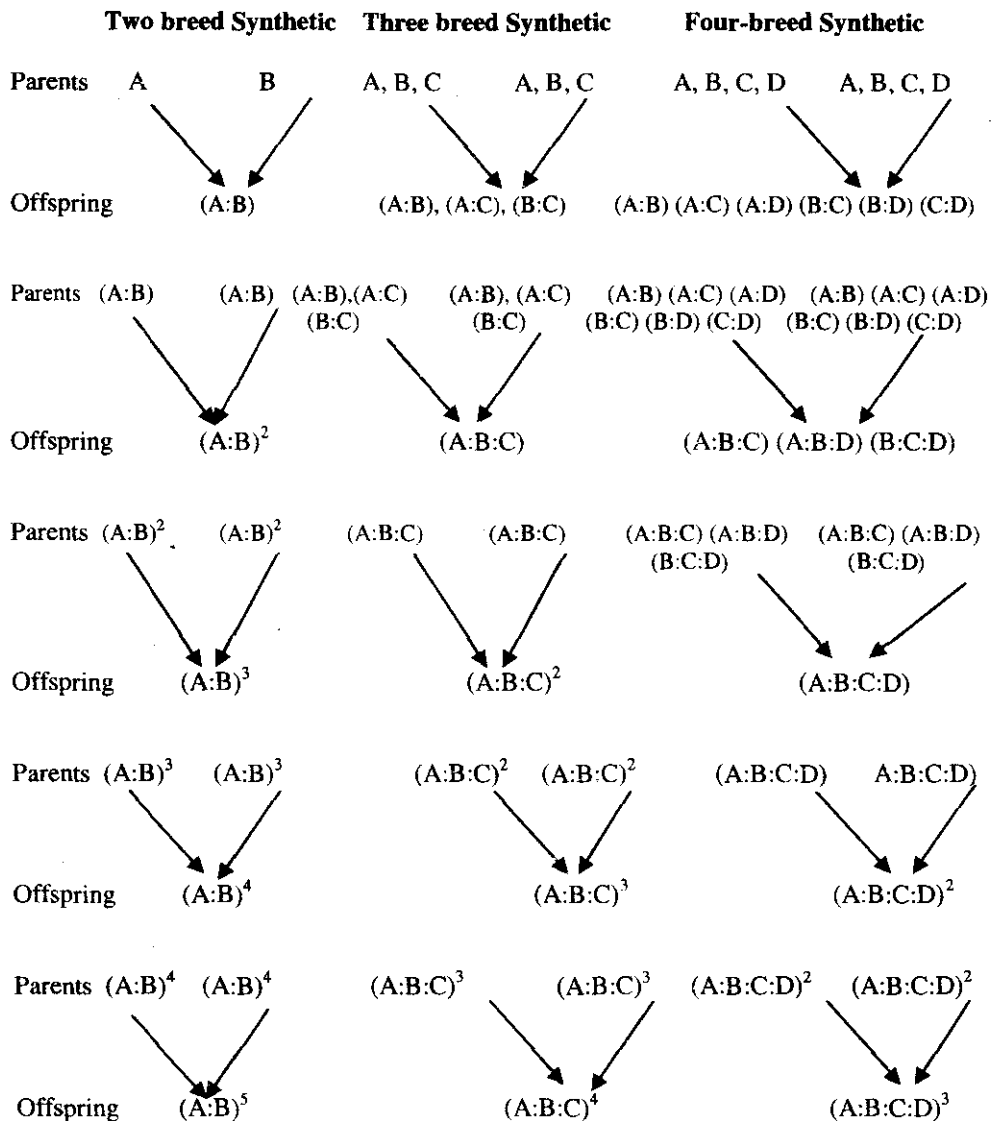
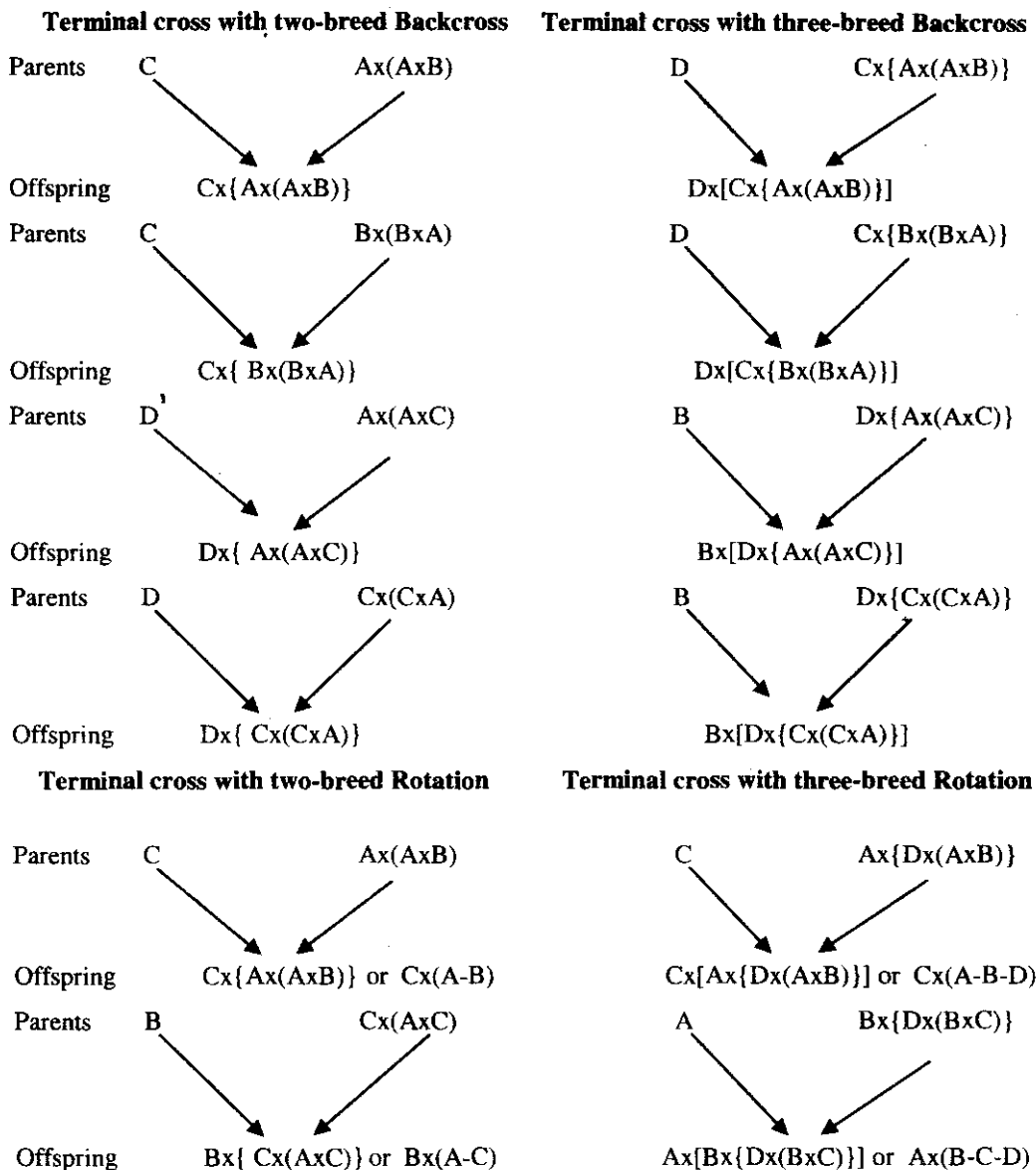


Figure 5. Two-, three- and four breed Synthetic population (with equal proportion of breeds).



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Figure 6. Terminal cross with two- and three-breed Backcross, Rotational cross and Synthetic.



Terminal cross with two-breed Synthetic Terminal cross with three-breed Synthetic

