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# CROSSING EXPERIMENTS FOR THE UTILIZATION OF SHEEP BREEDS IN NEW ZEALAND

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## SUMMARY

Some results from crossing experiments of relevance to the New Zealand sheep industry are examined in relation to the design and interpretation of experiments aimed at exploring the utilization of breed resources through crossbreeding. The problems of defining biological objectives, genetic change between generations, genetic-environmental interaction, adaptation, and experimental precision are briefly discussed in relation to the comparisons necessary for the estimation of genetic parameters of breed utilization.

DESPITE the emotional reactions that have frequently accompanied the concept of crossing strains and breeds for animal production (Rae and Wickham, 1970) crossbreeding has played an extremely important part in the evolution of breeds and continues to prove its usefulness in the production of commercial animals (Rae, 1952a, b). This would seem to be particularly true for sheep, some of the most highly organized crossbreeding occurring in the sheep industries of many countries despite a paucity of documented information on the relative merits of alternative breeds and crosses (Turner, 1967), and of the precise importance of hybrid vigour in crossbred performance. Experiments planned to evaluate these aspects have been reviewed by Turner and Young (1969), Burgkart and Averdunk (1969), and Hight and Jury (1970). The aim of this paper is to draw upon the results of but a few such experiments of relevance to the New Zealand sheep industry in order to discuss some features of their design and interpretation.

## TYPES OF CROSSBREEDING

Crossbreeding may be divided into two general categories according to whether the crossbred animals are produced anew in each generation, as is commonly the

case for lamb and mutton production, or whether they are retained for further breeding. In the latter case two further categories are commonly distinguished depending whether recourse is made to either of the parent breeds as in "grading up" to a different breed or in systematic rotational crossbreeding, or whether a new breed is formed directly from the crossbreds by interbreeding and selection.

In order to make decisions upon the ways in which breed resources may be utilized most efficiently, it is necessary to have information on the magnitude of the average genetic differences between the breeds, on the importance of hybrid vigour in crosses derived from them, and of the influence of maternal effects for all important aspects of economic performance. These are the basic genetic parameters of breed utilization. Prediction of the outcome of any particular crossing programme is of very limited accuracy unless reliable estimates of these genetic parameters are available.

#### GENETIC PARAMETERS OF BREED UTILIZATION

Hybrid vigour is usually defined as the difference in performance between the mean of the reciprocal crossbreds and the mean of their purebred parents. In the case of a cross between two breeds A and B, hybrid vigour (H) is estimated as:

$$H = \frac{\overline{AB} + \overline{BA}}{2} - \frac{\overline{A} + \overline{B}}{2}$$

where  $\overline{AB}$  and  $\overline{BA}$  represent the performance of the first-cross progeny out of B and A purebred females, respectively.

In addition to the average genetic component of breed and crossbred performance, it is necessary in mammals to consider separately a maternal component. Comparisons of purebred performance reflect the combined influence of both these components — *i.e.*, of the average genetic differences which exist between the breeds and of the different maternal environments they provide. This is because breed A offspring are reared under the maternal influence of breed A mothers alone, while breed B offspring are derived from only breed B mothers. Comparisons among the reciprocal crossbreds allow the two effects to be separated. Since the average genetic constitution

TABLE 1: MERINO-BORDER LEICESTER CROSSBREEDING  
(Results from McGuirk, 1967)

<i>Character*</i>	<i>Mean Performance</i>						<i>Breed Difference (Border-Merino)</i>		
	<i>Merino</i>	<i>Border</i>	<i>Merino</i>	<i>Border</i>	<i>Hybrid Vigour</i>		<i>Maternal Difference (Border-Merino)</i>	<i>Phenotypic</i>	<i>Genetic</i>
			×	×	<i>Hn</i>	<i>Hn/MP%†</i>			
Weaning wt. (lb)	56.5	72.3	69.8	67.4	4.2	7	- 2.4	15.8	18.2
EL/EJ	0.87	0.56	0.94	0.84	0.18	25	- 0.10	- 0.31	- 0.21
ELM/EL	0.34	0.60	0.80	0.50	0.18	38	- 0.30	0.26	0.56
LB/EJ	1.16	0.94	1.71	1.32	0.46	44	- 0.39	- 0.22	0.17
LW/EJ	1.11	0.80	1.59	1.26	0.47	50	- 0.33	- 0.31	0.02

\* EJ = number of ewes mated; EL = number of ewes lambing.

LB = number of lambs born; LW = number of lambs weaned.

ELM = number of ewes with multiple births (twins).

† MP = mean purebred performance.

of the reciprocal crossbreds is similar, their relative performance provides a measure of the different maternal environments provided by the two parental breeds. This permits the identification of the breed most suitable as the female parent in a crossing programme, while the consequent evaluation of the true genetic ranking of the breeds allows the more promising sire breeds to be identified.

#### COMPARISONS AMONG PURE BREEDS AND FIRST CROSSES

It is proposed to illustrate these points by considering some results from a reciprocal crossbreeding experiment (McGuirk, 1967) involving the Merino and Border Leicester breeds. Contemporary comparisons of the two purebreds and their reciprocal crosses gave the results shown in Table 1. Immediately obvious from these figures is the surprisingly low reproductive performance of the pure Border Leicesters, particularly the high proportion of dry ewes. McGuirk has commented that the situation was repeated in other years both in respect of the same ewes at subsequent lambings and the original Border Leicester dams of these ewes which were introduced from an outside stud flock. This perhaps bears out the warning issued by Donald (1955) on the importance of adaptation in breed and crossbred comparisons. He suggested that both imported stock and their progeny may require several years to reach a steady state of adjustment to new surroundings. A recent flock book survey of the Border Leicester breed (Trounson and Roberts, 1970), has, however, revealed a low net reproductive efficiency for this breed in eastern Australian stud flocks.

The other notable feature of McGuirk's results is the large difference between the performance of the reciprocal crosses, the maternal difference being in favour of the Merino dam for all characters. This difference, along with the estimates of hybrid vigour and of the phenotypic and genetic differences between the parental breeds, is also shown in Table 1. For the overall measures of reproductive performance (LB/EJ and LW/EJ) the maternal difference is of the order of 35% of the purebred mean but is as high as 64% for the measure of fecundity ELM/EJ, and only 4% for weaning weight. Only in the case of fecundity is the phenotypic reproductive performance of the Border superior to that of the Merino, although from the genetic point of view Borders are superior for all 4 reproductive characters except the proportion of dry ewes (EL/EJ).

Marked hybrid vigour is apparent for the reproductive characters, and as a percentage of the purebred mean its importance increases steadily from EL/EJ (25%) to LW/EJ (50%).

#### COMPARISONS AMONG INTERBRED $F_1$ CROSSES

The advantage of specifying performance in terms of genetic parameters lies in the ability to relate the relative performance of successive generations of pure- and cross-breeds. This is because the basic parameters can be interpreted in terms of their causal genetic components, allowing genetic theory to predict the extent to which they are expected to influence performance in different generations. Thus, hybrid vigour can be interpreted as a function of the square of the difference in gene frequencies for the parental breeds and of the degree of directional dominance for the loci affecting the character. This leads to the expectation that in the absence of selection an  $F_2$  generation formed by interbreeding  $F_1$  animals will exhibit only one half of the hybrid vigour shown by the  $F_1$ , and that because heterozygosity stabilizes in the  $F_2$  generation, no further reduction is expected in subsequent interbred generations (Falconer, 1960; Dickerson, 1969). However, as Falconer (1960) has clearly pointed out, the relative amounts of hybrid vigour expected in  $F_1$  and  $F_2$  generations are complicated by the existence of maternal effects. The same general pattern of change occurs for both the maternal and non-maternal components of performance, with the former component lagging one generation out of phase.

It needs to be emphasized that this is a simplified genetic model which has been chosen primarily to illustrate the consequences of hybrid vigour and maternal effects. More complete models which include sex-linkage, epistatic interactions and interactions involving maternal effects, have been presented by Dickerson (1969). Ignoring these complications and the effects of selection, the pattern of change in the population mean for a heterotic character subjected to a maternal effect is shown in Fig. 1. For this particular graph the assumption has been made that the amount of heterosis in the maternal component ( $H_m$ ) is 25% of that shown by the non-maternal component ( $H_n$ ). The effect of the heterosis in the separate components is clearly apparent from this graph, heterosis in the maternal component delaying the stabilization of overall performance until the  $F_3$  generation.

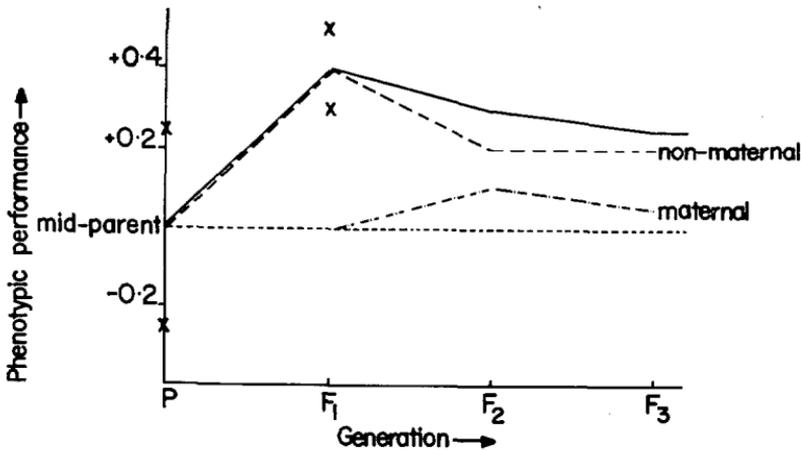


Fig. 1: Theoretical changes in performance from crossing and interbreeding without selection ( $H_n = 0.4$ ;  $H_m = 0.1$ ).

The actual shape of the overall change in phenotypic performance depends entirely upon the relative values of  $H_n$  and  $H_m$ . For this reason the actual unit of measurement of phenotypic performance is immaterial. Nevertheless, a scale appropriate to reproductive performance (e.g., LW/EJ) has been included in order to understand better the significance of the trends. Assuming respective values for  $H_n$  and  $H_m$  of 0.40 and 0.10, and a midparent of 0.70, the values for the  $F_1$ ,  $F_2$  and  $F_3$  generations are 1.10, 1.00 and 0.95, respectively. If the phenotypic difference between the parental breeds is of the order of 0.50, then the  $F_3$  stabilizes at the level of the better breed, as marked by the upper cross for the parental generation. If, however, the phenotypic difference between the breeds is less, the  $F_3$  level will exceed the value of the better breed, despite the absence of selection during its formation. It is, in fact, a general rule that the  $F_3$  animals are expected to stabilize at a higher level of performance than either parental breed if the sum of the heterosis for the maternal and non-maternal components is greater than the phenotypic difference between the purebreds.

One other feature displayed on this graph is the way in which the pattern of change over generations may vary according to the difference in maternal performance between the breeds. Thus a difference in maternal performance of 0.2 lambs/ewe could give an apparent level of performance for  $F_1$  animals at either of the second pair of crosses marked on the graph if only one of the reciprocal  $F_1$  crosses was available. If this was the case, then either

a slower or faster than expected change in performance from the  $F_1$  to  $F_2$  generations could be observed.

Some of the results of Hight and Jury (1970) on the reproductive performance of Romney and Border Leicester  $\times$  Romney ewes will now be examined in the light of these considerations.

For this experiment, heterosis in maternal performance ( $H_m$ ) may be estimated as  $2(F_2 - F_3)$ , but because of the lack of reciprocal  $F_1$  animals heterosis for the non-maternal component of performance ( $H_n$ ) cannot be determined. Instead, the best that can be done is to estimate a function comprising  $H_n$  and  $(MR - MB)$  from the relation:

$$H_n + (MR - MB) = 2(F_1 - F_2 + H_m)$$

where  $(MR - MB)$  represents the maternal difference between the Romney and Border Leicester breeds.

This has been done for some of the reproductive characters studied by Hight and Jury (1970), the results being presented in Table 2. As a percentage of the Romney mean the heterosis in maternal performance is -6% for ELM/EL, 4% for EL/EP and LB/EP, but 12% for LW/EP.

TABLE 2: BORDER LEICESTER-ROMNEY CROSSBREEDING  
(Results from Hight and Jury, 1970)

Character*	Maternal Heterosis		Non-maternal Heterosis plus
	$H_m$	$H_m/R\% \dagger$	Maternal Difference $H_n + (MR - MB)$
EL/EP	0.032	4	0.16
ELM/EL	-0.008	-6	0.14
LB/EP	0.04	4	0.32
LW/EP	0.10	12	0.50

\*EP = number of ewes present at lambing.

EL = number of ewes lambing; LB = number of lambs born.

LW = number of lambs weaned; ELM = number of ewes with multiple births.

$\dagger R$  = mean performance of purebred Romney ewes.

The values obtained for  $H_n + (MR - MB)$  would correspond to the amount of heterosis in the non-maternal component of each of these characters in the case of a zero maternal difference between the paternal breeds. The heterotic effect ( $H_n$ ) will be greater or less than these values, according to whether the maternal difference favours the Border Leicester or Romney breeds, respectively. It is interesting that preliminary results for the first year (1970) of a reciprocal crossbreeding experiment at the Woodlands Research Station indicate a maternal ad-

vantage in favour of the Romney over the Border Leicester of about 8% of the mid-breed mean for weaning weight (Clarke and Carter, unpubl.). This suggests that, for the Romney and Border Leicester breeds in this country, the maternal difference may indeed be in favour of the Romney although this could well depend upon the environment in which it is measured.

The values obtained for  $H_n + (MR - MB)$  may be apportioned between  $H_n$  and  $(MR - MB)$  and the corresponding phenotypic and genetic differences between the breeds calculated for each of the following three assumptions:

- (1)  $H_n = 0$
- (2)  $H_n = H_m$
- (3)  $(MR - MB) = 0$

The interesting result from such calculations is that, for each of these three situations, only in the case of ELM/EL is the Border Leicester breed both phenotypically and genetically superior to the Romney. Assuming that  $H_n$  is at least as great as  $H_m$  in absolute value, the phenotypic difference between the two breeds is surprisingly small for all characters except ELM/EL and is probably in favour of the Romney for EL/EP and LW/EP.

It seems, therefore, on the basis of the results of both McGuirk (1967) and Hight and Jury (1970) that the advantage of the Border Leicester breed in crossbreeding for improved reproductive efficiency rests upon an average genetic superiority in fecundity plus a heterotic advantage in all the broad components of reproductive efficiency and including fecundity. In view of the average values quoted by the survey of Burgkart and Averdunk (1970), it appears that hybrid vigour for fertility is particularly marked in crosses involving the Border Leicester breed. This is supported by the results of Pattie and Smith (1964).

The separation of heterotic and maternal effects for this type of experiment becomes possible by the inclusion of comparisons of first backcross performance (Dickerson, 1969). The method is thereby made particularly valuable for the evaluation of exotic breeds introduced through samples of males only.

#### REQUIREMENTS OF EXPERIMENTAL DESIGN

Many of the considerations relevant to experimental design have already been mentioned in the examples given and will be only briefly listed here.

### SAMPLING CONSIDERATIONS

In setting up breed utilization experiments, it is important that the parents of the crossbred generations constitute a representative sample of their breed in order to ensure generality of the results obtained. A minimum of 10 to 20 unrelated males has been suggested by the FAO Study Group (Anon., 1966). Representative sampling on the female side can be accomplished by securing animals from a wide geographic area, with the aim of assuring as wide a genetic (sire) background as possible. This, however, may make it necessary to reproduce the parental breeds in the test environment prior to the establishment of the experimental programme, in order to avoid bias due to lack of physiological adaptation.

It is also important to ensure that the gene complement of the crossbreds be comparable with that of the parental breeds. This means a need to avoid the deliberate selection of parents for the  $F_2$  and  $F_3$  generations and to minimize the effect of genetic drift between generations. The latter aspect also depends primarily upon the number of sires. In order to keep the rate of inbreeding down to the order of 1% per generation, at least 10 sires will be required and efforts will need to be made to ensure that each contributes a similar number of progeny to the next generation.

A further sampling consideration relates to the number of animals that need to be measured in order to detect differences with satisfactory precision. This has been discussed by Comstock and Winters (1942) and Dickerson (1969). The FAO Study Group (Anon., 1966) suggests a minimum of 30 to 60 animals per mean in each generation. Experimental precision can also be increased by arranging intra-sire comparisons of purebreds and crosses. An example of this is the production of contemporaneous  $F_1$  crossbreds and purebreds from the same or a similar sample of the purebred sires available. It is also important that records of performance be obtained for each experimental animal in order to permit tests of significance to be made and to provide estimates of genetic variability within breeds and generations.

### ENVIRONMENTAL CONSIDERATIONS

The experimental design should be such as to allow the genetic parameters to be estimated free of environmental bias. This may be accomplished either by ensuring that

the parental breeds and their crossbreds are reared together (Robertson, 1949) or that the performance of sequential  $F_1$ ,  $F_2$  and  $F_3$  generations are estimated as deviations from a control population of parental purebreds that are reproduced with minimum sampling effects. Age of dam, type of birth and rearing, and sex effects also need to be considered when designing mating plans, their interaction with type of mating effects frequently being of particular interest (Dickerson, 1969).

FAO Study Groups (Anon., 1966, 1968), Turner (1967) and Dickerson (1969) have all stressed the need to conduct breed utilization research under both typical current husbandry systems and improved husbandry conditions pertaining to the foreseeable future. This need depends, of course, upon the extent to which the genetic parameters of breed utilization change under altered environmental conditions, existing evidence indicating that gene  $\times$  environment interactions are likely to be important only for large genetic (*e.g.*, breed) and environmental differences (Turner, 1967; Turner and Young, 1969). The effect on breed performance of environmental changes induced by changes in market demand is also known to be important (Peren *et al.*, 1951; Hewitt, 1951).

The problem of foreseeing future environmental conditions affects not only the decision of which environments should be used for testing but also the biological objectives of the breed utilization study, and hence the records of performance that need to be kept. This has a profound bearing upon the research interests that need to be concerned with breed evaluation. Of particular relevance are those aspects of breed differences which reflect differences in the efficiency of animal production. The size of market lambs and the reproductive efficiency, maternal ability and size of the female parent all have a profound influence upon the biological efficiency of meat production (Hutton, 1963; Bowman, 1966; Dickerson, 1970; Large, 1970). Accordingly, experiments aimed at breed evaluation, while requiring to be soundly based in genetic terms, will also need to be carefully designed from a nutritional point of view in order that any important differences in biological efficiency may be clearly determined.

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