

T.S. Ch'ang* and R. Evans*

INTRODUCTION

Crossbreeding programmes of different complexity are formulated and used in various parts of the world with the objective to improve the biological efficiency of livestock production. A central theme of the crossbreeding strategy is the utilisation of heterosis (or hybrid vigour) which, as a measure of the superiority in performance of the F₁ crossbreds over the comparable purebreds, may originate from the sire, the dam and/or the progeny. There is evidence (Nitter, 1978) to suggest that different sources of heterosis (h) i.e. paternal (h^P), maternal (h^M), and individual (h^I), are involved in the superior lamb production performance observed to occur usually with crossbreeding. No published data, however, appear to be available on the comparative magnitude of these 3 sources of heterosis, or between each of them and the recombination effect (r^I, Dickerson, 1969) which may also be present in a crossbreeding programme for lamb production.

In Phase III of the CSIRO sheep crossbreeding experiment, a 3-year project (1979-1981/82) was undertaken to evaluate five heterosis utilisation breeding policies (Ch'ang and Atkins, 1981) in terms of 'total weight of lambs weaned per ewe joined' in a 3-breed (Dorset Horn, Merino, Corriedale) population. The purpose of this paper is to present the main results from the project with special reference to the comparative estimates of h^P, h^M, h^I, and their utilisation in formulating a breeding policy to maximise lamb production per ewe joined.

MATERIALS AND METHODS

(a) Sheep source and management

The records used in the study were obtained from a mix-aged (2 to 5 years old at lambing) pedigreed sheep population comprised of the 3 purebred and 6 F₁ crossbred groups, the latter were produced as contemporaries of the purebreds using the 3 x 3 breed diallel-mating design during Phase I and II of the experiment. It should be noted that according to this design, the same rams of a given breed were used to sire both the purebred and the F₁ crossbred progenies born in any one year. The experiment, since its inception, has been located on the CSIRO property 'Arding', in Armidale, N.S.W., Australia and the sheep are normally grazed all the year round on pastures with little or no supplementary feeding. However, during the drought in 1980 and part of 1981, supplements were fed as required (wheat for mature animals and hay for weaners).

* CSIRO Division of Animal Production, P.O. Box 239, Blacktown, NSW, 2148, Australia.

A total of 107 rams (63 purebreds and 44F₁ cross-breds) of the same age (2½ years old) were used over the 3-year study period in single-ram groups for annual mating in the autumn (5 weeks, May/June). In any one year, the mating groups were standardised with respect to age composition and number of ewes per ram. Lambing took place in the spring (October/November) and the lambs were weaned in January each year, at an average age between 12 and 13 weeks. At weaning, the lambs were individually weighed to the nearest 0.1 Kg and this record was used to calculate the 'total weight of lambs weaned per ewe joined'.

(b) Genetic composition of breeding policies

In the following development, the genetic parameters and coefficients used were those defined by Dickerson (1969). The five breeding policies, formulated to utilise different sources of heterosis, together with the genetic composition of their mean values are specified in Table 1.

Table 1. Breeding Policies and Their Genetic Composition[†]

Breeding Policy (BP)	Mating Design		Genetic Composition of Means (BP)
	♂	♀	
BP ₁	P ⁱ	x P ⁱ	(g ^I + g ^M + ε ^{H'}) = \overline{BP}_1
BP ₂	P ⁱ	x P ^j	$\overline{BP}_1 + h^I$
BP ₃	F ₁ ^{ij(ji)}	x P ^k	$\overline{BP}_1 + h^I + \frac{1}{2}r^I + h^P$
BP ₄	P ^k	x F ₁ ^{ij(ji)}	$\overline{BP}_1 + h^I + \frac{1}{2}r^I + h^M$
BP ₅	F ₁ ^{ij(ji)}	x F ₁ ^{ij(ji)}	$\overline{BP}_1 + \frac{1}{2}h^I + \frac{1}{2}r^I + h^P + h^M$

[†]Applicable to a 3-breed population under random mating.

In Table 1 above, P and F₁ denote purebred and crossbred respectively and i, j or k represents one of the 3 purebred breeds used. For example, F₁^{ij(ji)} ♂ x P^k ♀, (BP₃); means the F₁ ram(s) of the ith (paternal) and jth (maternal) breed cross is mated to purebred ewes of the kth breed to produce 3-way cross lambs.

(c) Statistical analysis

The experimental unit used in the statistical analysis was lamb production record of the ewe, and the data were analysed by least squares method (Harvey, 1964) using a linear model whose main effects are specified in Table 2. In the preliminary analysis, interactions between some of the main effects (Production year x Ewe population, Production year x Breeding policy within Ewe population) were included but found to be negligible and non-significant sources of variation and thus, had been omitted from the final model and analysis.

RESULTS

(a) Breeding policy effect

The least squares means for the different breeding policies and other fitted effects are presented in Table 2. Based on 2,020 degrees of freedom for error in the analysis of variance, all effects studied were statistically significant at the 1% level, except for the difference between BP₅ and BP₄, which was significant at the 5% level. The results from analysis of variance are not presented here to save space but may be inspected on request.

TABLE 2: Breeding policy effect on lamb production
(Total weight (kg) of lambs weaned per ewe joined.)

Effects studied	No. ewes	Least squares mean \pm standard error
Overall	2030	13.4 \pm 0.26
Production year:		
1979	724	13.3 \pm 0.42
1980	673	9.7 \pm 0.44
1981	633	17.2 \pm 0.45
Age of ewe at lambing:		
2-year-old	491	9.7 \pm 0.51
3-year-old	542	13.8 \pm 0.48
4-year-old	508	14.8 \pm 0.50
5-year-old	489	15.3 \pm 0.51
Ewe population:		
Purebred (PB)	794	11.2 \pm 0.41
F ₁ Crossbred (XB)	1236	15.6 \pm 0.32
Breeding policy (BP) [†]		
Within PB ewe population		
BP ₁	227	9.8 \pm 0.74
BP ₂	355	10.5 \pm 0.59
BP ₃	212	13.4 \pm 0.76
Within XB ewe population		
BP ₄	661	14.9 \pm 0.43
BP ₅	575	16.3 \pm 0.46

[†]BP₁ : utilises no heterosis
 BP₂ : utilisation of individual heterosis
 BP₃ : utilisation of paternal heterosis
 BP₄ : utilisation of maternal heterosis
 BP₅ : utilisation of heterosis from all sources

(b) Estimates of genetic parameters

The genetic composition for the means of the different breeding policies (Table 1) were equated to their least squares estimates (\overline{BP}_1 , Table 2) to yield five equations. h^I was estimated by $\overline{BP}_2 - \overline{BP}_1$; h^M and h^P were estimated from a pair of simultaneous equations derived from $\overline{BP}_4 - \overline{BP}_3$, and \overline{BP}_5 . Two alternative assumptions, (i) $r^I = -h^I$ and (ii) $r^I = 0$, were then used to yield solutions for h^M and h^P which are presented in Table 3.

TABLE 3. Comparative estimates of heterosis for lamb production per ewe joined

Genetic Parameters	ESTIMATE \pm S.E. [†] (Kg)		AS % OF \overline{BP}_1	
	$r^I = -h^I$	$r^I = 0$	$r^I = -h^I$	$r^I = 0$
h^I	0.74 \pm 0.94	0.74 \pm 0.94	7.6%	7.6%
h^P	2.53 \pm 0.62**	2.35 \pm 0.55**	25.8%	24.0%
h^M	4.01 \pm 0.62***	3.82 \pm 0.55***	40.9%	39.0%
TOTAL	6.54 \pm 0.87***	6.91 \pm 1.24**	66.7%	70.5%

[†]S.E. = Standard Error

** and *** denote significance at 1% and 0.1% respectively

DISCUSSION

The results presented in this paper are applicable to the experimental sheep population as a whole and may differ from those based on the constituent breed-combinations. It is therefore of some interest to compare the data presented in Table 3 with the average values from the published literature. Based on 24 and 23 estimates, the mean values of h^I and h^M for 'total weight of lambs reared per ewe exposed' were, according to Nitter (1978), 17.8% and 18.0% respectively, compared with 7.6% and 39.0% respectively from the present study ($r^I = 0$, Table 3). Between the corresponding estimates the difference appears substantial but, more importantly, the relative magnitude (as % of purebred mean) between h^I and h^M is not consistent within each set of estimates. No published data are available for comparison with the present estimate of the h^P effect on lamb production per ewe joined. The existing information therefore suggests that both the h^M and h^P effects are real and between them account for nearly 90% of the attainable heterosis in lamb production ($r^I = 0$, Table 3).

Utilisation of heterosis for improvement of lamb production by crossbreeding on an industry-wide scale presents operational problems as discussed by Nitter (1978) and Terrill (1974). The results from breeding policy study (Table 2) have provided experimental evidence, on a mini-industry scale, concerning the opportunity cost in terms of lamb production, of less than full utilisation of heterosis from all sources.

More specifically, within the purebred ewe population, there is little difference between BP2 and BP1, indicating that h^I effect by itself is relatively ineffective, but a substantial gain (+ 28%) in lamb production can be achieved simply by using F_1 rams as in BP3 compared with BP2, largely due to the occurrence of h^P effect. The average level of lamb production per ewe joined is considerably greater (+ 39%) in the F_1 crossbred (15.6 Kg) versus the purebred (11.2 Kg) ewe population. However, the utilisation of F_1 rams as in BP5 has resulted in a further significant increase (+ 9%), due to the occurrence in part at least of h^P effect. To what extent these findings obtained under Australian conditions are applicable to sheep populations and systems of production in different parts of the world is an open question, but the principle of utilising fully the additive nature of heterosis from different sources to maximise lamb production by crossbreeding, as in BP5, merits serious consideration for application in the industry.

SUMMARY

A central theme of applying the crossbreeding strategy to improve livestock production is the utilisation of heterosis which may originate from the sire, the dam and/or the progeny. Five breeding policies designed to utilise heterosis from different sources were experimentally evaluated in a 3-year study using 107 rams and 2,030 ewes. The mating design used also enabled crossbreeding parameters (h^P , h^M , h^I Dickerson, 1969) to be estimated as solutions of a set of simultaneous equations. The findings are discussed with reference to formulating a breeding policy to maximise the heterotic contributions to lamb production per ewe joined.

ZUSAMMENFASSUNG

Eins der wichtigsten Probleme beim Einsatz der Kreuzungsstrategie für die Verbesserung von Tierzucht ist die Verwendung von Heterosis, die von Vätertier, Muttertier und/oder Nachkommen entstammen kann. Fünf Zuchtschemen mit Anwendung von Heterosis verschiedenen Ursprungs wurden in einem dreijährigen Versuchsprogramm an 107 Widdern und 2030 Mutterschafen ausgewertet. Der verwendete Paarungsplan ermöglichte auch die Bestimmung von Kreuzungsparametern (h^P , h^M , h^I Dickerson, 1969) als Lösungen eines Simultangleichungssystems. Die Ergebnisse werden in Bezug auf die Entwicklung eines Zuchtschemas mit maximalem heterotischem Beitrag zum Lammungsertrag pro Mutterschaf diskutiert.

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