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Effect on fleece weight of combining genes from four flocks independently selected for increased fleece weight

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ABSTRACT

This study investigated whether heterosis was present when crossing sheep from four closed Romney flocks selected for increased fleece weight. Three of the flocks had been developed by AgResearch (C, W and H) and one by Massey University (M). Each ewe was joined with a single ram according to a diallel design to generate single-line, two-line and four-line cross progeny. The trial ran from 1988 to 1996 with 599 records available for analysis. In rank order, the mean (± standard error of mean) greasy yearling fleece weight (kg), adjusted for year, sex, pre-shearing live weight and days of wool growth was W (3.41 ± 0.08), H (3.39 ± 0.12), C (3.31 ± 0.10), M (3.10 ± 0.15) for the "single-line" groups, WC (3.40 ± 0.09), MW (3.36 ± 0.10), CH (3.24 ± 0.08), WH (3.16 ± 0.11), MH (3.14 ± 0.11), MC (3.14 ± 0.10) for the "two-line" crosses and 3.26 ± 0.06 for the four-line cross. Combining sheep from two or more flocks independently selected for increased fleece weight resulted, on average, in no heterosis in wool production among resultant progeny.

Keywords: Romney; selection, fleece weight; gene combination.

INTRODUCTION

Fleece weight is the crossbred wool trait that has the highest relative economic value (Wickham & McPherson, 1985). Although wool traits are not generally considered to exhibit sufficient heterosis to be of commercial significance to wool growers, it is conceptually possible that genes regulating different physiological pathways associated with a particular characteristic may segregate differently in closed populations selected solely for that characteristic. No studies are known to the authors where lines of sheep selected for increased fleece weight at different locations have been transferred to one site and interbred. In this study, samples of four closed Romney flocks that had been selected for increased greasy fleece weight at yearling shearing were transferred to, and maintained together at, one site over several breeding seasons while the lines were reciprocally crossed. The relative wool production of parental line, two-line and four-line cross progeny were compared to ascertain whether wool production of the two-line and four-line cross progeny exhibited sufficient heterosis as to be of commercial significance.

MATERIALS AND METHODS

Selection lines available

Subgroups of Romney ewes drawn from each of four selection lines were used. Replacement ewes and rams used for breeding in each flock had been previously selected over many years solely on the basis of their breeding value for yearling greasy fleece weight. Details of the flocks from which the sheep in this study were sourced are given below.

Massey University flock (M)

This selection line of approximately 80 ewes was established in 1956 using sheep from a flock developed by Massey Agricultural College to be representative of the Romney flocks in the southern North Island (Rae, 1958). The four rams in each lamb drop with the highest yearling fleece weight were used once as sires regardless of their own sire.

Hight flock (W)

This selection line of approximately 200 ewes was established at AgResearch Whatawhata Research Centre in 1967 using sheep from two flocks of Romney ewes that had been maintained at Whatawhata, representative of North Island Romney sheep. In 1981 the flock was reduced to about 125 ewes and transferred to the AgResearch Tokanui Research Station (Johnson *et al*., 1995). The flock was maintained as five sire-family lines from 1967.

Clarke flock (C)

This selection line of 150 ewes was established in 1973 at AgResearch Woodlands Research Station from a base flock comprising over 60 sources of Romney sheep from throughout New

Zealand (Clarke, 1974). In January 1991 half the flock was relocated to the AgResearch Tokanui Research Station. The flock was maintained as five sire-family lines from 1973.

Hawker flock (H)

This selection line of approximately 150 ewes was established in 1985 at AgResearch Woodlands Research Station by intensive screening of industry flocks, mostly in southern New Zealand, for yearling greasy fleece weight. The top 0.6% of 32,000 yearlings was screened during 1984 and 1985 (Hawker and Littlejohn, 1986). The flock was maintained as five sire-family lines from 1985.

Sheep management

The study commenced in February 1988 at the Whatawhata Research Centre, near Hamilton. Groups of ewes derived from the four base flocks and their progeny generated within the study were maintained under a single sire joining protocol.

All adult ewes in the study were grazed together, except during joining. Similarly the ram and ewe lambs born within the study were grazed as two single sex mobs between weaning and when they were shorn as yearlings.

In 1988 and 1989 groups of 12 aged ewes from each of the four selection lines were used. Superovulation was induced by hormone therapy and each ewe was joined with a single ram before being subjected to an embryo transfer procedure. Three new sires per line were used each year to generate progeny from four within-line and six two-line cross groups, according to a diallel design with respect to selection line and sex. The group of superovulated ewes was retained at Whatawhata with replacements added where deaths occurred. Between 1990 and 1995, additional aged ewes that were still structurally sound, were added to the within-line groups after they had been culled for age from within their respective base flocks. During this period each ewe was joined with a single sire under field conditions. Three new rams from each line were used each year. As in the first two years of the study, the ewes were allocated to their respective joining group according to a diallel design with respect to selection line and sex. Where more than three new rams per group were available for use, those with the heaviest yearling fleece weight were used. When insufficient new rams were available, one or more of the rams used the previous year were re-used. A total of 76 single-line rams and 218 single-line ewes were used with 16, 25, 18 and 17 rams and 30, 79, 78 and 31 ewes from the M, W, C and H flocks respectively leaving one or more progeny. Beginning in 1990 two-line cross rams and ewes born during the study were joined to generate a group of four-line cross progeny. A total of 30 two-line cross rams and 71 two-line cross ewes were used. Four-line cross ewes that were born during the study, were joined with unrelated four-line cross rams also born during the study. A total of 10 four-line cross rams and 24 four-line cross ewes were used. The study was terminated following the yearling shearing of sheep born in 1995.

Measurements

Lambs born within the study were weaned, drafted according to sex and shorn in early December each year. Yearling rams were shorn in August and yearling ewes were shorn in September each year.

The live weight of each sheep was recorded before yearling shearing and a fleece sample clipped from the midside region of the body for measurement of washing yield. Individual greasy fleece weight was recorded for all yearlings at each shearing and fleece-free live weight was calculated. Each wool sample was aqueous scoured and the washing yield calculated to derive an estimate of clean fleece weight.

Statistical analysis

Data were analysed by analysis of variance using GenStat (GenStat Committee, 2005). Live weight and washing yield were adjusted for effects of year of record, sex and interval between lamb and yearling shearing. Greasy fleece weight and clean fleece weight were adjusted for effects of year of record, sex, fleece-free live weight at the time of shearing and interval between lamb and yearling shearing.

RESULTS

A total of 599 fleece weight records were available for analysis. The numbers of yearling progeny of each "genotype" shorn each year are summarised in Table 1.

There was a significant slope between fleece-free live weight and greasy fleece weight ($b = 0.067 \pm 0.005$) and clean fleece weight ($b = 0.052 \pm 0.004$) vindicating inclusion of fleece-free live weight as a covariance term in the analysis model for these wool production measurements. Washing yield was not significantly related to fleece-free live weight and the term was not included in the analysis model for this parameter. Adjusted means ± standard error of mean for pre-shearing fleece-free live weight, greasy fleece weight, washing yield and clean fleece weight at yearling shearing for each of the "genotypes" generated within the study, are given in Table 2.

TABLE 1: Number of yearling sheep of each genotype shorn each year. M = Massey University selection line, W = Whatawhata selection line, C = Clarke selection line, H = Hawker selection line.

Year born	Parental line				Two-line cross						Four-line cross	Total
	M	W	C	H	MW	MC	MH	WC	WH	CH	MWCH	
1988	4	13	2	3	8	10	4	4	10	8		66
1989	2		1	6	7	5	6	1	7	11		46
1990	1	7	1		5	5	3	8	1	8	9	48
1991	1	2	2	4	6	7	3	5	7	9	13	59
1992	1	1	5	2		5	6	8	2	10	30	70
1993	3	7	3	4	3	4	3	10		4	46	87
1994		3	1	1	2	5	2	2	3	1	46	66
1995	2	58	40	4	1		1	2		2	47	157
Total	14	91	55	24	32	41	28	40	30	53	191	599

TABLE 2: Mean ± standard error of mean for fleece-free live weight at yearling shearing adjusted for effects of year of record, sex, and interval between lamb and yearling shearing, and yearling greasy fleece weight, washing yield and clean fleece weight adjusted for effects of year of record, sex, fleece-free live weight at the time of shearing and interval between lamb and yearling shearing. M = Massey University selection line, W = Whatawhata selection line, C = Clarke selection line, H = Hawker selection line.

Genotype	Fleece-free live weight (kg)	Greasy fleece weight (kg)	Washing yield (%)	Clean fleece weight (kg)
Parental line				
M	35.3±1.2	3.10±0.15	74.6±1.2	2.26±0.13
W	32.2±0.6	3.41±0.08	74.5±0.7	2.54±0.07
C	31.8±0.7	3.31±0.10	76.2 ± 0.8	2.52±0.09
H	35.8±1.0	3.39±0.12	76.2 ± 1.0	2.59±0.10
Two-line cross				
MW	35.5±0.9	3.36±0.10	74.3±0.8	2.51±0.09
MC	35.7±0.8	3.14±0.10	73.8±0.8	2.31±0.08
MH	36.1±0.9	3.14±0.11	74.0±0.8	2.32±0.09
WC	34.4±0.8	3.40±0.09	76.3±0.7	2.59±0.08
WH	35.4±0.9	3.17±0.11	74.8±0.8	2.37±0.09
CH	35.2±0.7	3.25±0.08	75.7±0.6	2.45±0.07
Four-line cross				
MWCH	34.6±0.4	3.26±0.06	74.9±0.4	2.44±0.05
Parental line effect	**	NS	†[1]	NS
Two-line effect	NS	*	**	*

[1] P<0.1

Estimates of heterosis, expressed as the percentage change between individuals and the mean of their parents, for each of the measured characteristics following crossing the parental lines and two-line cross groups, are given in Table 3. The level of significance in Table 3 indicates whether the estimate of heterosis is significantly different from zero.

Yearlings born within the M and H lines were heavier at yearling shearing than yearlings born in the W and C lines (Table 2). There were no differences in fleece-free live weight between the two-line crosses or between the two-line crosses and the four-line cross, all of which were heavier than the W and C lines but not significantly different from the M and H lines. Crossing the M and C lines and the W and C lines were the only crossings that resulted in significant heterosis for fleece-free pre-shearing live weight (Table 3).

Adjusted greasy fleece weight of the M group was lighter than the W and H groups but not significantly different from the C group (Table 2). Rank order for greasy fleece weight of the two-line cross groups was WC, MW, CH, WH, MH and MC with the greasy fleece weight of the WC and MW groups being heavier than the MH and MC groups (Table 2). There was no significant heterosis for greasy fleece weight following any of the crossings (Table 3).

Rank order for decreasing washing yield within the single-line groups was C, H, M and W with the difference between the C and W groups approaching significance. Similarly the rank order for washing yield for the two-line cross groups was WC, CH, WH, MW, MH and MC with the yield for the WC group being higher than the yield for the MW, MH and MC groups (Table 2). There was no significant heterosis for washing yield following any of the crossings (Table 3).

Rank order for adjusted clean fleece weight within the single-line groups was (H, W, C, and M with the clean fleece weight of the M group being significantly lighter than the other three groups. The rank order for clean fleece weight within the two-line cross groups mirrored the order for greasy fleece weight of WC, MW, CH, WH, MH and MC with the clean fleece weight of the WC and MW groups being heavier than the MH and MC groups (Table 2). There was no significant heterosis for clean fleece weight following any of the crossings (Table 3).

TABLE 3: Relative change ± standard error of mean for adjusted mean values of the parental lines for fleece-free live weight at yearling shearing, yearling greasy fleece weight, washing yield and clean fleece weight occurring as a result of crossing the parental and two-line crosses of lines individually selected for increased yearly greasy fleece weight. M = Massey University selection line, W = Whatawhata selection line, C = Clarke selection line, H = Hawker selection line.

Genotype	**Fleece-free live weight**		**Greasy fleece weight**		**Washing yield**		**Clean fleece weight**	
	Relative change (%)	Significance	Relative change (%)	Significance	Relative change (%)	Significance	Relative change (%)	Significance
Two-line cross								
MW	5.2 ± 3.3	NS	3.4 ± 4.1	NS	-0.4 ± 1.4	NS	4.5 ± 4.7	NS
MC	6.5 ± 3.2	*	-2.1 ± 4.1	NS	-2.1 ± 1.4	NS	-3.5 ± 4.7	NS
MH	1.5 ± 3.4	NS	-3.3 ± 4.4	NS	-1.8 ± 1.5	NS	-4.2 ± 5.1	NS
WC	7.7 ± 2.8	*	1.3 ± 3.3	NS	1.3 ± 1.2	NS	2.3 ± 3.8	NS
WH	4.3 ± 3.2	NS	-6.8 ± 3.9	†[1]	-0.7 ± 1.2	NS	-7.6 ± 4.3	†[1]
CH	4.2 ± 2.8	NS	-3.1 ± 3.4	NS	-0.6 ± 1.2	NS	-4.1 ± 3.8	NS
Four-line cross								
MWCH	-2.2 ± 1.5	NS	0.5 ± 2.1	NS	0.7 ± 2.4	NS	0.1 ± 0.7	NS

[1] P<0.1

Adjusted pre-shearing fleece-free live weight, yearling greasy fleece weight, washing yield and yearling clean fleece weight of the four-line cross were not significantly different to the mean of the parental lines or the two-line crosses (Table 2). There was no significant heterosis for any of the measured characteristics following crossing two-line crosses to form a four-line cross (Table 3).

DISCUSSION

Each of the parental selection lines sub-sampled for this study was maintained with a randomly selected control flock of a similar size to the selection lines. The control flock was derived from the same base flock or flocks as the selection lines themselves (Clarke & Johnson, 1993). This enabled the realised genetic progress in increasing greasy fleece weight to be calculated as 0.034, 0.047, 0.058 and 0.020 kg per year in the M, W, C and H lines respectively (Clarke & Johnson, 1993; Wuliji *et al.* 1998). Initially the M, W and C lines and their respective control lines were each randomly selected from industry flocks, with no screening for fleece weight. While the H line and its associated control flock were selected from the same flocks, the intensive screening process applied to the H line resulted in a selection differential of 0.66 kg of the H line over its control line in the first year (Wuliji *et al.*, 1998). Ewes from the H flock that entered this study in its initial years were a sample of the ewes screened from industry flocks and subsequently culled from the selection flock on account of their age. As samples of the four control lines have never been run at a common location, no information is available to evaluate their relative productivity as an indicator of the "starting point" for each of the selection lines. Notwithstanding the between-line differences in productivity, estimates of heterosis derived from the balanced diallel cross design used in this study will be unbiased (Griffing 1956).

Closed selection lines are expected to have a higher homozygosity for the characteristics in question than the population at large. Inbreeding associated with the small size of the selected population may also result in increased homozygosity for genes regulating other characteristics. Crossing of closed lines reintroduces heterozygosity and advantages associated with general fitness (Falconer 1960). The longest kept line sampled in this study had been maintained for 32 years, or approximately 9 generations. This relatively short number of generations provided limited opportunity for homozygosity to increase significantly, however some heterosis was evident in pre-shearing fleece-free live weight following crossing of the single-line groups. Two-way line crosses were nearly 5% heavier, on average, than their respective parental lines. Published studies of two-way breed crosses also indicate hybrid vigour for early lamb and hogget growth, typically of the order of 5 - 10% (Clarke, 1982). Only about half of the liveweight advantage of the two-way line crosses was retained by the four-line cross.

For liveweight-adjusted fleece weights, no advantage of two-way and four-way line crosses over their parental lines was evident. Under a dominance model of heterosis this indicates no evidence for line differences in the frequency of genes or genotypes affecting wool production relative to body size, and/or no evidence of directional dominance for these genes (Falconer, 1960). We are unaware of any published estimates of crossbreeding effects on these traits, although heterotic effects of the order of 5 to 10% have been observed for fleece weight unadjusted for variations in live weight at shearing (Clarke, 1982). In this study two-way line crosses showed, on average, positive heterosis for fleece weight unadjusted for live weight, but only of the order of 2.5%. It was significant for only WC and MW crosses (7-9% of their parental line mean) suggesting positive directional dominance effects for genes affecting this trait and frequency differences in these genes between these pairs of parental lines.

The intensive screening for greasy fleece weight applied when establishing the H line, and possible carry-over flock of origin effects, may have influenced the performance of crosses involving H sheep which had mean greasy fleece weights that tended to be lighter than the mean of their parent lines. No other reason can be suggested why wool growth of the MW two-line cross should be any greater than that of any of the other six two-line crosses apart from chance variation in a small subset.

Thus, in summary, this study showed that combining sheep from two or more flocks which had previously been independently selected for increased fleece weight gave low heterosis for live weight at shearing but no significant heterosis for wool production independent of live weight. Assuming similar trends and similar estimates of within group variation, group sizes would have needed to have been approximately four times greater to detect statistical significance for heterosis effects in wool production relative to body size. Despite this apparent lack of initial heterotic advantage, longer term advantages in improved selection response, through changes in gene frequency for genes with additive effects on wool production relative to body size could nevertheless accrue to breeders from crossing sheep from different superior lines, a topic which was beyond the scope of this experiment.

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