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Genetic and environmental parameters for lambing behaviour in Merino lines divergently selected for ewe multiple rearing ability

S.W.P. CLOETE[AB], J.B. VAN WYK[A], A.J. SCHOLTZ[B] AND A.R. GILMOUR[C]

[A]Free State University, PO Box 339, Bloemfontein 9300, South Africa

ABSTRACT

Data were recorded for lambing behaviour of approximately 1000 Merino ewes lambing over a 10-year interval from 1993 to 2002. The resource population was divergently selected from the same base population since 1986, either for (H line) or against (L line) maternal multiple rearing ability. Line differences ($P < 0.05$) favoured H line ewes for length of parturition and maternal cooperation score. Heritability was estimated at 0.17 ± 0.04 for length of parturition, 0.11 ± 0.04 for maternal cooperation score and 0.20 ± 0.04 for the interval ewes remained on or near to the birth site. A small service sire effect for length of parturition in ewes amounted to 0.03 ± 0.02. Maternal cooperation score was genetically related to the time spent on or near to the birth site (0.53 ± 0.18). Genetic divergence between lines was detected in all three traits. These results and the obtained parameter estimates indicate that selection for improved multiple rearing ability was feasible in paddock-reared sheep flocks.

Keywords: Selection; lamb survival; maternal ability; breeding values.

INTRODUCTION

Lamb mortality is a major constraint to efficient sheep production (Haughey, 1991). Selective breeding was advocated as a means of improving lamb survival and ewe rearing ability under paddock conditions (Lindsay *et al*., 1990; Haughey, 1991). Behavioural adaptations were contended to contribute to selection responses in lamb survival in the pastoral areas (Alexander, 1988). Very few published estimates of genetic (co)variances for peri-parturient behaviour in sheep have been published (Hinch, 1997). Breed and line differences in some traits (e.g., length of parturition and neonatal progress of lambs – see Alexander *et al*., 1990; Cloete & Scholtz, 1998; Kuchel & Lindsay, 1999) may indicate genetic variation. Genetic (co)variances for lambing and neonatal behaviour for lambs of South African dual-purpose breeds were reported recently (Cloete *et al*., 2002). Low to medium levels of direct and maternal genetic variation were found in this study.

This study reports results pertaining to genetic factors associated with peri-parturient behaviour of sheep. The resource population used in the study was divergently selected for maternal multiple rearing ability over a number of years (Cloete & Scholtz, 1998).

MATERIALS AND METHODS

Two lines of Merino sheep were divergently selected from the same base population since 1986, using maternal ranking values for lambs reared per joining. Ewe and ram progeny of ewes rearing more than one lamb per joining (i.e., reared twins at least once) were preferred as replacements in the High (H) line (Cloete & Scholtz, 1998). Replacements were preferably descended from ewes rearing fewer than one lamb per joining (i.e. ewes were barren or lost all lambs born at least once) in the Low (L) line. Depending on the average reproduction of the lines and replacement needs, progeny of ewes that reared one lamb per joining were occasionally accepted in both lines. Selection decisions were mostly based on three or more maternal joinings, especially in the case of rams. Once selected, ewes remained in the breeding flock for at least five joinings, unless in the case of death or severe teeth or udder malfunction.

Details of the experimental site and husbandry practices followed can be obtained from Cloete & Scholtz (1998).

The lambing flock was observed continuously by one or two trained observers for a period of approximately three weeks during peak lambing (Cloete & Scholtz, 1998). Observations took place during 1993 – 2002. Behavioural recordings included length of parturition (calculated as the period between the first definite sign of parturition and the birth of the last lamb). Ewes that experienced difficult births were assisted on an objective basis, as described by Cloete *et al*. (2002) and Cloete & Scholtz (1998). The birth site of individual ewes was identified with a peg. Ewes were scored for active co-operation by standing still, adopting a slightly hunched posture to enable access to the udder and nudging the lamb in a position to facilitate suckling. The frustration of the first suckling attempts of their neonates by backing, circling or butting was also recorded (Alexander, 1988). These recordings were combined for lambs to obtain an overall ewe maternal co-operation score on a six-point scale, and averaged for ewes bearing multiples. Ewes were regarded as having left their birth sites permanently after having moved away more than 15 m for more than 2 h (Cloete & Scholtz, 1998). Numbers of records were 1117 for length of parturition, 1034 for maternal behaviour score and 1003 for the interval on the birth site. The percentage of ewes giving birth to multiples were 50.5 % in the H line and 33.9 % in the L line. Time intervals were transformed to natural logarithms prior to analysis to normalise the distribution.

The ASREML program (Gilmour *et al*., 1999) was used for the estimation of the fixed effects, and also subsequently to derive variance components for behavioural traits in univariate analyses. Fixed effects

[B]Elsenburg Agricultural Centre, Private Bag X1, Elsenburg 7607, South Africa
[C]NSW Agriculture, Orange Agricultural Institute, Orange 2800, NSW, Australia

included year of lambing (1993-2002), selection line (H and L), number of lambs given birth to (single or multiple) and ewe age (two to seven and older years). Operational models were obtained by fitting combinations of these effects and interactions between them. Random terms were then added, resulting in the following models for analyses:

$$y = Xb + Z_1a + e \quad (1)$$
$$y = Xb + Z_1a + Z_2c_{PE} + e \quad (2)$$
$$y = Xb + Z_1a + Z_3c_{sire} + e \quad (3)$$

In these models, y was a vector of observations for ewe behavioural traits, b, a, c_{PE} and c_{sire} were vectors of fixed effects, direct genetic variances, ewe permanent environmental variances and random service sire variances respectively, X, Z_1, Z_2, and Z_3 were the corresponding incidence matrices relating the respective effects to y, and e the vector of residuals. The assumptions were as before. All analyses included the full pedigree file, consisting of 4351 individuals, the progeny of 216 sires and 1107 dams.

Log likelihood tests were conducted to determine the most suitable model for each trait in uni-variate analyses. Subsequently, two-trait animal models were fitted. All relevant direct and permanent environmental correlations between traits were estimated, together with their standard errors.

Breeding values for traits were computed using the formerly obtained heritability estimates, and averaged within birth years from 1986 to 2002 to obtain genetic trends. These breeding values were obtained from analyses where selection line and its interactions with other traits were excluded from the operational model. This was because the inclusion of selection line as fixed would scale the breeding values for genetic differences between lines that accrued as a result of selection. In the case of time intervals, the overall phenotypic mean was added to the averaged breeding values prior to transformation back to the normal scale. These averaged breeding values on the normal scale were then expressed as deviations from the overall phenotypic mean.

RESULTS

Selection line did not interact ($P < 0.05$) with the other fixed effects. The births of H line ewes were 6.3% shorter ($P < 0.05$) than those of their L line contemporaries (Table 1). Maternal co-operation score was correspondingly higher in H line ewes ($P < 0.05$). The period that ewes remained on the birth site was independent of selection line, although H line ewes tended to remain longer ($P < 0.25$).

Heritability (± SE) was estimated at 0.17 ± 0.04 for length of parturition. The service sire variance ratio, although resulting in a significant ($P < 0.05$) improvement in the likelihood ratio, amounted to only 0.03 ± 0.02. Further h^2 estimates were 0.11 ± 0.04 for maternal cooperation score and 0.20 ± 0.04 for the period that ewes remained on or near the birth site. Ewe permanent environmental effects were not significant for any of the traits. Genetic, phenotypic and environmental correlations between traits measured were relatively low. The exception was the genetic correlation between dam cooperation score and the period that ewes stayed on or near their birth sites, which amounted to 0.53 ± 0.18.

Regressions of breeding values on birth year for length of parturition declined in the H line and increased in the L line (P for divergence between lines < 0.05; Table 2).

Breeding values for maternal co-operation score on year of birth increased ($P < 0.05$) in the H line, while a tendency towards a decline ($P = 0.06$) was observed in the L line (P for divergence < 0.05). With regard to the

TABLE 1: Least squares means (± SE) for length of parturition, cooperation score and the interval ewes remained on or within 15 m from their birth sites. The time intervals were transformed to natural logarithms prior to analysis. Backtransformed means are given in parentheses.

Effect	Length of parturition (min)	Cooperation score (n)	Stay on birth site (min)
Number of observations	1117	1034	1003
Overall mean	3.97 ± 0.07 (53)	5.37 ± 0.07	6.63 ± 0.06 (279)
Selection line:	*	*	P<0.25
H Line	3.84 ± 0.08 (47)	5.54 ± 0.08	5.71 ± 0.08 (302)
L Line	4.10 ± 0.09 (60)	5.20 ± 0.09	5.56 ± 0.09 (260)

* Denote significant ($P < 0.05$) line differences

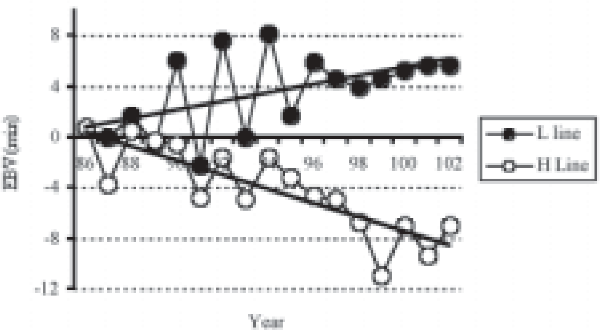
TABLE 2: Details of linear regression equations depicting genetic change as reflected by the regression of averaged breeding values on year of birth for traits that were measured on ewes

Trait and line	Slope (b ± SE)	Slope % of mean	Intercept(a ± SE) (a ± SE)	r
Length of parturition (min)				
H Line	-0.563[a] ± 0.096	-1.06*	0.40 ± 0.90	0.84
L Line	0.333[b] ± 0.133	0.63*	0.79 ± 1.2	0.54
Maternal cooperation score (n)				
H Line	0.0058[b] ± 0.0017	0.11*	0.024[b] ± 0.016	0.45
L Line	-0.0066[a] ± 0.0033	0.12	-0.059[a] ± 0.031	0.21
Stay on birth site (min)				
H Line	0.884[b] ± 0.429	0.32	-6.7 ± 4.0	0.47
L Line	-1.529[a] ± 0.646	-0.55*	-3.4 ± 6.1	0.52

[a,b] Denote significant ($P < 0.05$) differences between selection lines for slopes or intercepts

* Denote significant ($P < 0.05$) regressions

FIGURE 1: Estimated breeding values (EBV) for length of parturition in High (H) and Low (L) line ewes, averaged within birth years.



period spent by ewes on or near the birth site, regressions of breeding values on birth year tended (P = 0.06) to increase in the H line and declined (P < 0.05) in the L line. Trends for length of parturition are illustrated in Figure 1.

DISCUSSION

Length of parturition in ewes was heritable (0.17). Breeding values pertaining to this trait in the two selection lines also showed divergence in the present study. These results suggest that ease of birth can be manipulated genetically. This contention is supported by indirect evidence reporting differences in ease of birth (and/or the occurrence of dystocia or parturient deaths) between breeds (Alexander *et al*., 1990; Cloete *et al*., 1998), or between lines within breeds (Haughey, 1983; Knight *et al*., 1988; Cloete & Scholtz, 1998).

Although the effect was small (3% of the overall phenotypic variance), service sire effects resulted in an improved log likelihood when length of parturition was analysed. The heritability of deaths due to dystocia was higher than for other sources of death when paternal halfsib procedures were applied (Smith, 1977). In a study involving Marshall Romney (selected for rearing ability) and Control Romney lines, parturient deaths were higher in lambs sired by Control Romney rams than in those sired by Marshall Romney rams (Knight *et al*., 1988). This effect was, however, more pronounced in the Control Romney ram by Marshall Romney ewe combination.

Maternal cooperation score had a small genetic component. The line differences in the interval from standing to suckling in lambs found previously in the same resource population (Cloete & Scholtz, 1998), could partly have resulted from the divergent selection pressure for multiple rearing ability on maternal cooperation score. Our previous results indicated that H line ewes were less likely to circle and back than L line contemporaries. They were also more likely to adopt a posture to facilitate suckling. The environment provided by the dam in SA Mutton Merino lambs contributed to the ability of lambs to suckle successfully within a reasonable period of time (Cloete *et al*., 2002). In an embryo transplant study by Kuchel & Lindsay (1999), superfine-wool lambs cared for by medium-wool ewes showed faster neonatal progress than their contemporaries cared for by superfine-wool ewes. The percentage of lambs marked was correspondingly affected, being markedly lower in superfine-wool lambs cared for by superfine-wool dams.

The period that ewes remained on or near the birth site was heritable, and there was genetic divergence between lines for this trait. Ewes in the H line tended (P < 0.25) to remain longer on or near their birth sites than L line contemporaries. Szantar-Coddington (1994) found that fertility-flock Merino ewes remained on their birth sites for 266 minutes compared to 251 minutes for control ewes. Knight *et al*. (1989) found that 41 Marshall Romney ewes grazed from their birth sites 46 minutes after birth, while 16 control Romneys did so after 27 minutes. Significance was not demonstrated, but the general pattern from all three studies was that ewes selected for rearing ability tended to remain on their birth sites for longer periods. This behaviour facilitates the formation of a strong mother-offspring bond (Alexander, 1988). Divergence in the interval ewes remained on or near their birth sites may thus be expected as a correlated response to selection.

Maternal cooperation score was genetically related to the period that ewes remained on or near their birth sites. No comparable results were found in the literature. It is well established that the birth site is of utmost importance in the formation of a strong dam-offspring bond (Murphy *et al*., 1994). Early neonatal lamb-ewe interactions are equally important in the formation of this bond (Lindsay *et al*., 1990; Murphy & Lindsay, 1996). When assessed from this perspective, such a relationship seems to be reasonable.

CONCLUSIONS

The obtained line differences and genetic trends suggested that behaviour in the H line was adapted to enhance lamb survival, when patterns identified by Alexander (1988) as being important were considered. Lamb survival, and in particular the survival of multiples, was correspondingly improved in the H line (Cloete & Scholtz, 1998). This study contributes to a better understanding of factors associated with lamb survival, and mechanisms involved in the genetic improvement of rearing ability in pasture-fed ewes. This provides a basis for the improvement in the long-term viability of sheep farming through the establishment of genotypes that are capable of rearing their offspring with minimal external inputs (Lindsay *et al*., 1990; Haughey, 1991).

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