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The ability of Merino ewes and lambs to reunite after separation, as affected by divergent selection for ewe multiple rearing capacity

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Abstract. Lambs and ewes from 2 Merino lines that had been selected divergently from the same base population for (High line) or against (Low line) multiple rearing success, were assessed for their ability to reunite after temporary separation. Selection in the lines began in 1986, and data for this study were obtained from 1998 to 2002. Postnatal lamb mortality for lambs born during 1998–2002 were generally lower ($P<0.05$) in high line lambs than in low line contemporaries. When tethered 20 m away from their dams at 1 day of age, lambs in the High line tended ($P<0.10$) to be more likely to bleat and tug on the tethering rope than Low line contemporaries. Dams of lambs in the high line were quicker ($P<0.05$) to reunite with a tethered lamb than low line ewes. They were also quicker ($P<0.05$) to establish contact with the full litter after separation of multiples. In an experiment conducted in pens at an age of 3 days, no line difference was found for the ability of ewes to reunite with their lambs or litters when confronted by a choice of 3. When lambs were assessed in the same way, 89% was able to reunite with their dams within 5 min, with no evident line difference ($P>0.05$). When released from the pens, the dams of 95% of single lambs returned for their lambs, the proportion tending ($P<0.10$) to be higher in the High line than in the Low line. The dams of multiple lambs returned for 73% of the lambs tested, with no clear line difference. Lambs in the High line were more ($P<0.01$) likely to follow next to the front legs or midside of their dams than Low line lambs. Line differences in some behavioural patterns in favour of the High line are considered to be conducive to lamb survival when compared with Low line performance.

Additional keywords: behaviour, discriminate, follow, lamb vigour, parameter estimates, recognition, survival.

Introduction

Lamb mortality is regarded as 1 of the most important sources of reproductive wastage in sheep (Alexander 1988; Haughey 1991) and a 'core' level of lamb loss remains, even if managerial inputs are optimised (Alexander 1984). A better understanding of the cause of lamb loss is required if such wastage is to be reduced (Lindsay *et al*. 1990).

Lambs are precocious in the neonatal stage, and are normally able to follow their dams shortly after birth (Le Neindre and Poindron 1990). Their survival, however, depends strongly on an exclusive bond between dam and offspring that is established soon after birth (Alexander 1988; Lindsay *et al*. 1990). Visual, olfactory and auditory clues contribute to the ability of dams to identify offspring that they have bonded to during the neonatal phase (Alexander 1988; Le Neindre and Poindron 1990; Lindsay *et al*. 1990).

The ability of lambs to identify and stay with their dam is also important. Stevens *et al*. (1984) and Nowak and Lindsay (1990) suggest that lambs are attracted to ewes as soon as 12 h after birth. Some lambs are able to discriminate between their own and alien dams at this stage. In this respect, crossbred lambs performed better than pure Merinos (Stevens *et al*. 1984; Nowak and Lindsay 1990).

Selective breeding has been advocated by several authors as a means of improving the lamb survival, and thus overall flock productivity (Le Neindre and Poindron 1990; Lindsay *et al*. 1990; Haughey 1991). Genetic parameter estimates are scarce for behavioural attributes conducive to lamb survival (Hohenboken 1986; Hinch 1997). Selective breeding has, however, been shown to be effective in reducing lamb mortality, particularly in multiple births (Cloete and Scholtz 1998). The effect of divergent selection for multiple rearing performance of Merinos on the ability of ewes and lambs to reunite after separation was investigated in the present study. The data were concurrently used for the estimation of genetic parameters.

Material and methods

Animals, management and location

Two lines of Merino sheep have been divergently selected from the same base population since 1986. Details regarding the establishment of the lines and selection procedure of replacements were reported by Cloete *et al*. (2004). Ewe and ram progeny of ewes rearing more than

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1 lamb per joining were generally preferred as replacements in the high (H) line. Replacements in the low (L) line were preferably descendants of ewes rearing fewer than 1 lamb per joining. Selection of rams was mostly based on ≥3 maternal joinings. Ewes remained in the breeding flock for 5 joinings, unless death occurred or severe teeth or udder malfunction were noted.

Since their establishment, the 2 lines have been maintained as a single flock, except during joining when they were separated into sire groups with 4–6 rams. For the duration of this study, the selected lines were maintained on the Elsenburg experimental farm near Stellenbosch. The experimental site and husbandry of the animals are detailed in the literature (Cloete *et al*. 2002*b*, 2004).

Lamb birthweight and mortality

Birthweights of 1281 lambs born between 1998 and 2002 were obtained within 24 h of birth. The mortality of these lambs in postnatal stage (between birth and weaning, excluding those deaths that occurred before and during birth) was also recorded.

Recording behavioural data

The study was conducted over 5 years (1998–2002). The paddocks used and management of ewes at lambing have previously been described (Cloete and Scholtz 1998; Cloete *et al*. 2002*b*). Data for this study were recorded at 2 stages, between 12 and 36 h after birth (1 day) and between 60 and 84 h after birth (3 days). The treatment of experimental animals was related to procedures used by Alexander *et al*. (1990*b*), and involved 2 persons. The handler worked with the animals, while the recorder observed ewe and lamb behaviour and recorded the applicable data. Data were collected annually over about 3 weeks during peak lambing. About 64% of all lambs born were assessed. Recordings at 1 day of age were conducted in the lambing paddocks, and involved:

(i) The handler approached ewes cautiously, to minimise disturbance. A lamb was then removed from the ewe and the handler hid the lamb from the sight of the ewe behind his body. In some instances, particularly with single-bearing ewes, the mother followed the handler closely. The handler and recorder moved in a criss-cross pattern to confuse such ewes. The lamb was then tethered (using a peg stuck firmly in the ground) about 20 m away from the ewe. The estimation of distances was aided by a grid reference system in the paddock (Cloete and Scholtz 1998). After tethering, the handler moved at least 20 m away from the lamb, to limit interference. The activity of the tethered lamb (standing still, lying, bleating, tugging on the tethering rope) was recorded on the binomial (yes or no) scale. The time that ewes took to reunite with individual lambs was recorded to the nearest second; and

(ii) Multiple lambs (including 30 viable triplets produced by 11 triplet-bearing ewes) were tethered in sequence, and additional recordings were made. Recordings included the following of ewes by litter members not tethered, and the waiting of ewes for the free lamb(s) on the way to the tethered lamb, on the binomial scale. The time that ewes took after reaching the tethered lamb to establish contact with all members of a litter was recorded. The establishment of contact with other litter members was defined as looking back to lambs following within 2 m, or the nosing/licking/nuzzling of such lambs.

For the recordings at 3 days of age, a set of movable pens was erected near the experimental site (Fig. 1). The pen consisted of a reception area, consisting of a 2.7 × 2.7 m pen (area A). This area led to a holding area, where ewes and lambs to be tested were kept (area B). Gates with corrugated iron sides were fitted to the side of these pens leading to the rest of the facility (denoted by the bold line in Fig. 1). A third pen of dimensions 5.4 × 5.4 m (area D) separated these pens from 3 smaller 1.35 × 1.35 m pens, numbered 1 to 3. A second external pen of 2.7 × 2.7 m was erected next to this facility in order to be visible from the smaller pens, but removed from it by at least 5 m (area C). This facility was used in the following manner.

(i) Sets of 3 ewes were put individually in pens 1–3, while the remaining ewes and lamb were kept in area A. The lambs belonging to the 3 ewes were put in area C, to be visible from the smaller pens. The activities of these ewes were recorded over a period of at least 1 min. Behaviour patterns identified were grazing, bleating and the seeking of lambs within the pen on the binomial scale. The latter behaviour involved rapid turning in the pen and sniffing at the ground and sides.

(ii) Lambs were subsequently moved to area B. They were then individually released in area D, at a spot denoted by the arrow (Fig. 1). The time they took to reunite with their dams in pens 1–3 was recorded. Reuniting was defined as remaining in close contact for at least 10 s, nuzzling the head of the ewe, and attempts to pass through the bars of the small pen to be with the dam.

(iii) Positions of the ewes and the lambs were subsequently reversed, with the ewes being put in Area B and individual single lambs or the full litter in pens 1–3. These proceedings were conducted out of sight of the ewes. The ewes were then individually released into Area D, and the interval required to reunite with their lambs or litters was recorded. An attempt was regarded as successful when a ewe remained in close contact, nuzzling or sniffing at the lamb(s) for at least 10 s, and attempted to reach through the bars of the gate to groom her lamb(s).

(iv) Individual ewes were then returned to area B. The lamb(s) belonging to a specific ewe were placed in pen 3. The appropriate dam was then released, chased to the outlet of the facility, and left to go. Upon returning to pen 3 searching for their offspring and establishing contact, a lamb was passed over the sides of the pen. This process was repeated for each individual lamb in litters.

(v) After this test, lambs were chased with their dams over a distance of at least 10 m. The position they adopted in following their dams was

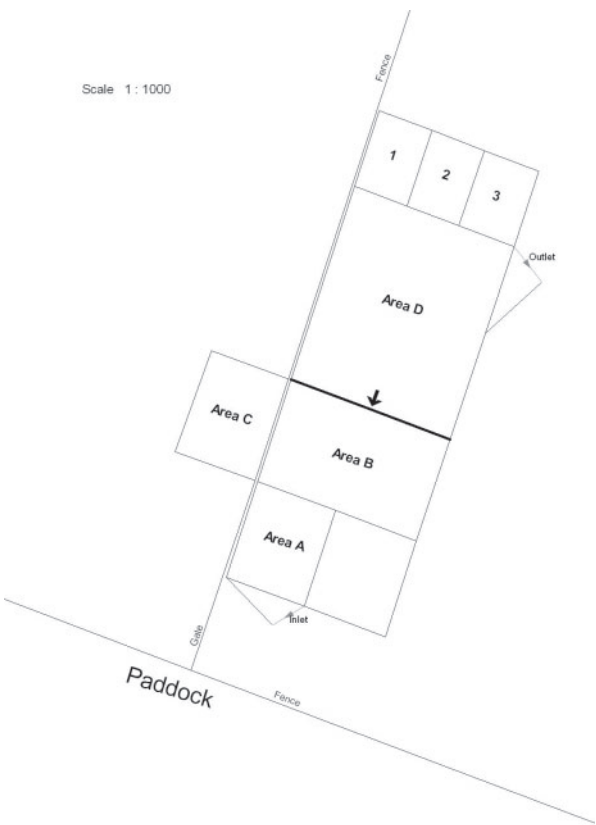

Figure 1. Schematic diagram representing the ground plan of the facility used during the testing of 3-day-old lambs.

recorded as next to the front legs or next to the midside as compared with next to or behind the hind legs of the ewe.

In all cases where time intervals were recorded, 5 min were regarded as a cut-off time. In ewes or lambs failing to achieve the objective in time, a terminal value was recorded. In total, behavioural data at 1 day of age were available for 812 lambs, while 791 records were available at 3 days of age.

Statistical analyses

Differences in proportions measured on the binomial scale were assessed for statistical significance by Chi-squared procedures (Siegel 1956). Observed frequencies were fairly high in all comparisons, and the Yates correction for continuity was not applied. According to Sokal and Rohlf (1981), this correction involves an unduly conservative test in large samples. Data based on time intervals were skewed and transformed to natural logarithms before analysis. Least-squares procedures were used to assess these data statistically, to account for uneven subclasses. The ASREML statistical package (Gilmour *et al*. 1999) allows the estimation of a range of random effects in animal breeding, while also predicting estimates of appropriate least-squares means for selected fixed effects. All analyses were conducted from the perspective of the lamb and fixed effects included selection line, birth year, gender (male or female), age of dam (2–7 years) and birth type (single or multiple). Least-squares means were obtained for all fixed effects, but only means for line effects were tabulated. Results pertaining to the other effects were only presented in cases where significant interactions with selection line were observed.

Longitudinal data, where a specific trend is expected, can be described very effectively by the usage of smoothing splines (Verbyla *et al*. 1999). Trends with regard to birth year were thus modelled on the assumption that selection could have resulted in a specific trend, using cubic splines in ASREML (Gilmour *et al*. 1999). The splines initially consisted of 3 components: a fixed linear component, random deviations from linearity conforming to a smooth trend, and random deviations from linearity not attributable to a smooth trend. Linear and nonlinear components of the splines for birth year were interacted with selection line, to assess differences in these trends between lines. Where such interactions were significant, trends were obtained from analyses involving splines, while least-squares means and standard errors were obtained from analyses where year was treated as fixed. Pedigrees of 2702 animals born from 1993 to 2002 were available, and used to compute random animal and dam effects. Log-likelihood ratios were used to determine goodness of fit for several models involving direct additive as well as maternal genetic or permanent environmental variances (Cloete *et al*. 2002*a*).

Results

Postnatal lamb mortality

About two-thirds of 866 H line lambs that were assessed were multiples. In the low line, slightly below 50% of 347 lambs were born as multiples (Table 1). Lamb mortality of single lambs was not significantly influenced by selection line ($P = 0.19$). In multiples, however, H line progeny sustained lower levels of mortality compared with L line contemporaries ($P<0.01$).

Observations at 1 day of age

Lamb birthweight did not differ ($P>0.10$) between selection lines (Table 2). When lambs were tethered, no marked line differences were observed in activity. The proportion of lambs which bleated among the 608 lambs from the H line tended to be higher ($P = 0.06$) than that found in 204 lambs in the L line (0.96 *v.* 0.92). There was also a tendency ($P = 0.08$) for lambs in the H line to tug on the tether rope more often than those in the L line (0.87 *v.* 0.82). Among multiple lambs not tethered, 405 H line lambs tended ($P = 0.11$) to follow their dams to the tethered sibling more often than 89 L line contemporaries (0.85 *v.* 0.79).

Dams of lambs in the H line reunited with their lambs after a shorter ($P<0.05$) interval than L line ewes (Table 2). This generalisation was complicated by an interaction between selection line and the linear component of the spline for the birth year of the lamb (Fig. 2). The interval required to reunite H line lambs and ewes decreased over years, while a slight increase was observed in L line lambs. Dams of multiple H line lambs were quicker ($P<0.01$) to establish contact with the full litter after reaching a tethered lamb, than dams of multiple L line lambs (Table 2). Dams of 378 H line multiples were more ($P<0.05$) likely to reunite with the full litter within 5 min of reaching a tethered lamb than the dams of 77 L line lambs (0.77 *v.* 0.65).

Observations at 3 days of age

When ewes were penned within sight of a group of lambs at 3 days of age, no distinct line differences in their activity were recorded ($P>0.10$). Practically all ewes (99%) bleated for their lambs and looked in the direction of the pen containing them.

Selection line did not affect traits recorded at 3 days of age (Table 2), but interacted with the nonlinear component of the spline fitted to birth year for the interval required by the dams of penned individual lambs or litters to reunite with these lambs ($P<0.05$; Fig. 3). In absolute terms, means for the intervals required by the dams of L line lambs to reach their lambs or litters were slightly above those required by the dams of H line lambs for 1998 and 1999. During 2000, dams of H line lambs took longer ($P<0.05$) to reunite with their lambs or litters than dams of L line lambs. In 2002, however, dams of H line lambs again had a distinct advantage ($P<0.05$) in this regard when compared with those in the L line.

Table 1. Postnatal (deaths from birth to weaning, excluding deaths occurring before and during birth) lamb mortality of single and multiple born H and L line ewes during the years 1998 to 2002

Classification	Selection line		Chi-square
	H line	L line	
Singles			
No. of lambs surviving birth	289	184	
Postnatal deaths	0.11	0.15	1.74
Multiples			
No. of lambs surviving birth	577	163	
Postnatal deaths	0.25	0.44	21.34*
Overall			
No. of lambs surviving birth	866	347	
Postnatal deaths	0.20	0.29	9.52*

*$P<0.01$.

Table 2. Least-square means (± s.e.) depicting the effect of selection line on birthweight and the measures of behaviour considered during the study

Behaviour traits were analysed after transformation to natural logarithms; back-transformed means are in parentheses
Values within each row followed by the same letter are significantly different at $P = 0.05$

Trait	Selection line	
	H line	L line
Birthweight (kg)	3.97 ± 0.09	3.95 ± 0.11
Number of observations	909	372
Observations at 1 day of age		
Interval to reunite with tethered lamb	3.28 ± 0.11 (27)a	3.68 ± 0.14 (40)a
Number of observations	608	204
Interval to establish contact with full litter	2.92 ± 0.24 (18)b	3.62 ± 0.31 (37)b
Number of observations	378	77
Observations at 3 days of age		
Interval for ewe to reach lamb/litter	2.17 ± 0.14 (9)	2.01 ± 0.19 (8)
Number of observations	398	154
Interval for lamb to reach ewe	3.44 ± 0.13 (31)	3.49 ± 0.15 (33)
Number of observations	595	196

When released from the pens, the dams of 95% of singles returned for their lambs. The dams of 202 H line singles were more ($P<0.05$) likely to return than those of 112 L line contemporaries (0.97 *v.* 0.92). No line difference was found for multiple lambs, where the dams returned for 73% of their lambs. The dams of multiples were less likely to return for subsequent lambs when accompanied by 1 lamb. When chased away together with their dams after the pen test, a higher ($P<0.01$) proportion of the 588 H line lambs followed their dams next to the front legs or mid side than 195 L line contemporaries (0.59 *v.* 0.39). Lambs from the latter group were more likely to follow behind or at the hind legs of the dam.

Parameter estimates

Additive heritability estimates (h^2) were not significant, except for birthweight (Table 3). Estimates of maternal effects (m^2) were significant, with the exception of the interval required by ewes to reunite with their 3-day-old lamb(s) in the pens. Estimates of m^2 for recordings at 1 day of age exceeded 0.20, both for the interval to reunite with a tethered lamb and to establish contact with all litter members in multiples. The partitioning of maternal variances into direct and permanent environmental components did not result in improvements in log-likelihood ratios where m^2 were significant. The inclusion of direct-maternal covariance components similarly did not result in improved log-likelihood ratios.

Discussion and conclusions

Postnatal lamb mortality

Higher mortality levels are normally expected with an increase in multiple birth rate (Haughey 1991). However,

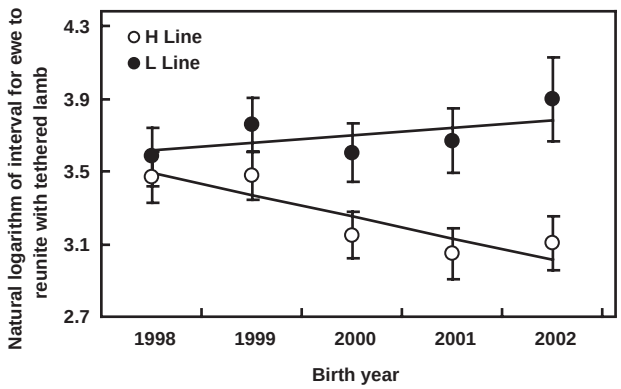

Figure 2. The interaction between the fixed linear component of the spline for lamb birth year and selection line regarding the time required for ewes to reach their tethered lambs at 1 day of age for the high (H) line (○) and low (L) line (●). Vertical bars represent the standard error of the mean.

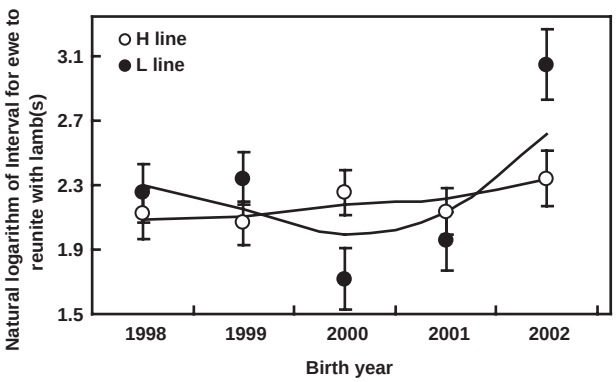

Figure 3. The interaction between the random nonlinear component of the spline for lamb birth year and selection line regarding the time required for ewes to reach their lambs or litters at 3 days of age for high (H) line (○) and low (L) line (●). Vertical bars represent the standard error of the mean.

lamb survival in the H line was not compromised despite a higher birth rate. In fact, the survival of multiples was higher in the H line, as was reported previously on the same resource population (Cloete and Scholtz 1998).

Behavioural observations

Improved maternal care of 1-day-old lambs by H line dams was demonstrated by their ability to reunite more rapidly with a tethered lamb than L line dams. This trait strengthened with further divergence between lines during the study period. Given the moderate estimate for m^2, it is conceivable that the observed line difference stems from indirect genetic selection that took place in the lines. Breed differences are commonly used as an indication of genetic variation in a specific trait if limited information is available on genetic parameters, as is the case with the traits considered. Results pertaining to different breeds (Alexander *et al*. 1990*b*) were inconclusive in a study where the Merino, Border Leicester and a Border Leicester derived line selected for rearing ability (Glen Vale) were compared. Merino dams were quicker to reach tethered lambs than the other breeds, but a higher proportion of Merinos failed to reach a tethered lamb within the time allocated. Glen Vale ewes were quicker to reach their tethered lambs than Border Leicester ewes. Merino ewes able to collect their full litters within 5 min took longer to do so than either Glen Vale or Border Leicester ewes. When it is considered that the Glen Vale line was also selected for rearing ability, these results seem to support those obtained in the present study. An alternative line of reasoning would be that previous experience of caring for multiples enhanced the ability of higher reproducing H line ewes to care for multiples, as was reported for New Zealand Romney ewes (Alexander *et al*. 1984). Twin-bearing 2-year-old Romney ewes that had twins as yearlings, resembled mature ewes with multiple twin-rearing records in a deliberate separation test within 2 days of parturition. Primi-parous 2-year-old ewes and contemporaries with singles at yearling age were less likely to move to a tethered lamb, and took longer to reach it than the above-mentioned groups of ewes with previous experience in the care of twins. Further research on the partitioning of the observed line response in the present study in genetic and environmental components is indicated.

There were tendencies (P<0.10) suggesting that 1-day-old H line lambs were more active when tethered, as reflected by bleating and escape attempts compared with L line lambs. It has been established that bleats by lambs are invariably followed by a bleat by the dam (Lindsay *et al*. 1990). The ability of lambs to distinguish between their own mothers and alien dams was related to their frequency of bleating (Nowak 1989). It is thought that this continuous stimulus–response behaviour pattern facilitates the establishment of a strong dam–offspring bond (Lindsay 1996). There was also a tendency towards better following behaviour in 1-day-old H line lambs. This trend was augmented by results obtained at 3 days, when H line lambs were more (P<0.01) likely to follow next to the front legs or midside of their dams, while L line lambs were more likely to follow next to the hind legs or behind the ewe. All these findings seem to indicate a greater vigour in H line lambs, as suggested by a previous result that H line lambs progressed quicker from standing to suckling than L line contemporaries (Cloete and Scholtz 1998). Support for following behaviour contributing to lamb survival, comes from a study on a goitre-affected flock, where following behaviour and survival were impaired in lambs with higher thyroid scores (Alexander *et al*. 1990*a*). Fewer (P<0.05) 1-day-old Merino singles and twins followed their dams than Border Leicester and Glen Vale contemporaries (Alexander *et al*. 1990*b*).

Alexander *et al*. (1990*b*) found no breed differences between Merino, Border Leicester and Glen Vale ewes to reunite with their lambs at 3 days of age. Both Alexander *et al*. (1990*b*) and this study suggest similar results. One possible explanation is the lack of genetic variation and line differences. Nearly 90% of all lambs used in the pen tests at 3 days of age were able to reunite with the correct dam within 5 min, with no difference between lines. In the absence of

Table 3. Variance components and ratios for the traits considered

σ^2_a, direct additive; σ^2_m, maternal additive; σ^2_e, environmental variances; h^2, direct heritability; m^2, maternal heritability

Trait	Variance components			Variance ratios (± s.e.)	
	σ^2_a	σ^2_m	σ^2_e	h^2	m^2
Birthweight	0.0934	0.1822	0.2075	0.19 ± 0.08	0.38 ± 0.04
Traits at 1 day					
Interval for ewe to reach lamb	0.0549	0.2525	0.8110	0.05 ± 0.05	0.23 ± 0.05
Interval to contact with full litter	0.2164	0.6855	1.9137	0.08 ± 0.09	0.24 ± 0.07
Traits at 3 days					
Interval for ewe to reach lamb	0.1151	n.s.	1.2470	0.09 ± 0.07	n.s.
Interval for lamb to reach ewe	0.0667	0.2344	1.2776	0.04 ± 0.05	0.15 ± 0.05

n.s., not significant (P>0.05) according to log-likelihood value.

published reports directly comparable with the present study, several results depending on the comparison between breeds are cited. In this respect, Nowak and Lindsay (1990) reported that more Border Leicester × Merino lambs were able to identify their Merino dams at 12 h of age than purebred Merinos. The formation of an exclusive dam–offspring bond evolves rapidly during the first 3 days of life (Poindron *et al*. 1996). It is possible that initial line differences in this behavioural attribute could be masked by 3 days (when the tests were conducted in the present study), since the formation of an exclusive dam–offspring bond is well developed at this stage.

No apparent explanation can be given for the interaction ($P<0.05$) of the nonlinear components of the spline for year with selection line (Fig. 3). The result may be coincidental, since numbers of progeny tested in this line are limited by a relatively low overall reproduction (Cloete *et al*. 2004), a smaller ewe flock, and a greater likelihood of lambs to succumb during birth (Cloete and Scholtz 1998). Ewes in the L line also lambed later in the season (Cloete *et al*. 2004), decreasing the likelihood of substantial numbers of lambs being included in a study conducted during peak lambing. The percentage of L line lambs born per year and being tested at 3 days of age ranged from 33 to 64% of all lambs born. These percentages were higher and more stable in the H line, between 59 and 73% of all lambs born being tested.

Finally, results from this study support the hypothesis that the behaviour of ewes and lambs in the H line differed in some ways from that of L line contemporaries. According to the classification by Alexander (1988), these differences are all likely to benefit lamb survival. Previous studies on the same resource population came to similar conclusions regarding other behavioural traits (Cloete and Scholtz 1998; Cloete *et al*. 2003), as well as observed levels of lamb mortality (Cloete and Scholtz 1998).

Parameter estimates

Very few formal estimates of genetic parameters are available for behavioural traits (Hinch 1997). Recent analyses at this institute indicated direct and/or maternal genetic variation in length of parturition as well as the intervals from birth to standing and from standing to suckling in lambs of dual-purpose breeds (Cloete *et al*. 2002*a*). It thus comes as no surprise to find significant maternal variance components for the majority of the behaviour traits analysed in this study. These results imply that favourable alleles for these traits can be transmitted to future generations. A significant maternal component for the time required by individual 3-day-old lambs to reunite with their dams indicates that the contribution of the dam to form a strong bond enabling the reunion of lambs with the correct dam is important. No comparable estimates to test these results against were found in the literature.

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