# Lamb survival in Australian Merino Sheep: A genetic analysis[1,2]

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**ABSTRACT:** Direct and maternal components of variance for lamb survival to birth, 7 d, and weaning (110 d) were estimated by REML procedures in a flock of Australian Merino sheep. A total of 14,142 lambs, the progeny of 421 sires and 3,666 dams, born between 1975 and 1983 were available for analysis. The study has produced some of the most precise estimates of genetic parameters for lamb survival in the Australian Merino. Very low heritabilities for lamb viability (0.03) and the performance of the dam or ewe rearing ability (0.07) suggest that genetic solutions to lamb survival are unlikely to be significant. But, despite the low heritabilities, there is still potential for improvement through selective breeding. The estimated repeatability of at least 0.10 shows that multiple records on the rearing ability of a ewe over its lifetime can increase selection accuracy. More importantly, such repeatabilities indicate that current generation improvement can be achieved by culling ewes from the breeding flock with poor rearing ability. Despite maternal bond score and lamb birth weight being highly repeatable and moderately heritable traits, correlations with lamb survival were essentially zero. These traits therefore have no value as indirect selection criteria for Merino lamb survival.

**Key words:** genetics, lamb survival, Merino sheep



J. Anim. Sci. 2010. 88:3198–3205
doi:10.2527/jas.2009-2461



## INTRODUCTION

Lamb loss between birth and weaning in Australian Merino sheep has been estimated to be more than 30% based on discrepancies between reproductive potential based on ultrasound pregnancy scanning and achieved marking percentages in studies of commercial flocks (Kilgour, 1992; Kleemann and Walker, 2005). Given the complexity of lamb survival and the extensive Merino production systems in Australia, selecting sheep with a genetic propensity for lamb survival is a very beneficial and desirable option. Including lamb survival in the breeding objective offers a permanent low-cost solution provided there is genetic variation and effective selection criteria are developed with favorable correlations with survival.

Genetic improvement of reproduction has typically focused on selection for the ability of ewes to rear multiples (Atkins, 1980; Cloete and Scholtz, 1998; Cloete et al., 2004). However, improvements in lamb survival are unlikely if litter size is increased through selection without any regard to whether the additional lambs born can be successfully reared (Lindsay, 1982) as multiple-born lambs are more likely to die than singles (Hatcher et al., 2009). When determining the contribution of genetic variation to lamb survival, it is necessary to consider the direct genetic effect due to the genes of the lamb and the maternal effect of the dam, which has genetic and environmental components (Bradford, 1972). Direct heritability of survival in Merino sheep, or lamb viability, has been estimated to be very low (Piper and Bindon, 1977) with low estimates reported in other breeds (Barwick et al., 1990; Gama et al., 1991; Lopez-Villalobos and Garrick, 1999; Morris et al., 2000; Safari

[1]Phenotypic aspects of lamb survival, including birth type, sex, age of dam, flocks, and the nonlinear relationship between birth weight and lamb survival, were reported in Hatcher et al. (2009).

[2]The skilled assistance of staff at the Trangie Agricultural Research Centre (Trangie, New South Wales, Australia) in record collection and management is gratefully acknowledged, especially the contributions of A. M. Burns, K. J. Flinn, I. M. Rogan, and S. J. Semple. This research was supported by a grant from the Wool Research Trust Fund on the recommendation of the Australian Wool Corporation. The Cooperative Research Centre for Sheep Industry Innovation provided the funds to allow this analysis to proceed. K. J. Thornberry (Industry and Investment NSW, Orange Agricultural Institute, Orange, New South Wales, Australia) assisted with data preparation before analysis. N. M. Fogarty (Industry and Investment NSW, Orange Agricultural Institute) provided valuable advice during revision of this manuscript.

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Received September 8, 2009.
Accepted June 14, 2010.

et al., 2005b; Riggio et al., 2008). Most reports of the maternal component of survival, or ewe rearing ability, suggest that it may be greater than the direct genetic effect (Lopez-Villalobos and Garrick, 1999; Morris et al., 2000; Riggio et al., 2008), but not all concur (Barwick et al., 1990; Burfening, 1993) due to differences in analytical techniques and models. More recently it has been suggested that genetic variation in lamb viability is influenced by lamb age with estimates declining with time after birth (Southey et al., 2001; Sawalha et al., 2007; Riggio et al., 2008).

This study describes genetic analyses undertaken on a mixed bloodline genetic resource flock that represented the major strains and bloodlines within the Australian sheep industry. A detailed description of the data and fixed effects was reported by Hatcher et al. (2009), who identified a nonlinear relationship between birth weight and lamb survival with light and heavy birth weight lambs more likely to die. This paper presents estimates of the magnitude of direct and maternal genetic variation of lamb survival in Australian Merino sheep. Lamb deaths were classified into periods of loss between birth and weaning so that the influence of age on genetic variation could also be investigated. The genetic relationships between lamb birth weight and maternal behavior and lamb survival at each time period were also estimated.

## MATERIALS AND METHODS

Although there was no Industry & Investment NSW ethics committee in existence at the time of this study, all procedures reported in this paper would meet the current guidelines stipulated by the Australian Code of Practice for the Use of Animals for Scientific Research.

Data were collected from a flock maintained by New South Wales Department of Primary Industries at the Agricultural Research Centre, Trangie (31°59′ S, 147°57′ E) on the central western plains of New South Wales, Australia. The sheep and the lamb survival records were described by Hatcher et al. (2009). The pasture was predominantly native grasses with some lucerne pastures grown in rotation with a dry land cropping program. General animal husbandry was as described by Morley (1951) and the composition of the 15 subflocks and general management by Mortimer and Atkins (1989). Briefly, the predominant Merino strains in Australia (fine-wool 2 bloodlines, medium-non-Peppin 2 bloodlines, medium Peppin 10 bloodlines, and strong wool or broad micron 1 bloodline) were represented by the 15 subflocks with a total of 14,142 lambs born between 1975 and 1983 available for analysis. These lambs were the progeny of 421 sires and 3,666 dams. The annual size of each subflock was 3 rams and 100 ewes with rams used for 1 mating only with links between subflocks. Ewes were first mated at 2 yr of age and allowed 5 further annual opportunities to lamb with culling only due to extreme physical disability or black-wooled progeny. Lambing occurred during July and August each year with lambing rounds conducted twice daily. During each lambing round, lambs were identified with their dams within 12 h of birth, ear-tagged, and weighed. Any dead lambs were noted at this time. A maternal bond score was assigned to each ewe that coded the behavior of the ewe toward the lamb at tagging and ranged from 1 (good, maintaining close contact with lamb) to 4 (poor, ignoring lamb). A roll call of surviving lambs was made at approximately 7 d of age (range 5 to 8 d) when ewes and lambs were moved from the lambing paddocks, after marking at approximately 30 d of age (range 3 and 5 wk) and at weaning when the average age was 110 d.

Variance components for cumulative survival at birth (1 d), 7 d, marking (30 d), and weaning (110 d), and survival within these time periods were obtained by REML procedures with a linear mixed animal model using ASReml (Gilmour et al., 2006). An earlier phenotypic analysis of these data identified low repeatability of dam performance or ewe rearing ability in the 7- to 30-d and 30- to 110-d periods, indicating that lamb survival beyond the first 7 d of age is largely outside the control of the ewe (Hatcher et al., 2009). Therefore these 2 periods were combined into one for the genetic analysis (i.e., 7 to 110 d).

Safari et al. (2005a) reported that direct and maternal genetic variances can be underestimated when analyzed using an animal model on the logit scale leading to smaller estimates of heritabilities. However, Lopez-Villalobos and Garrick (1999) reported close agreement between their logit and probit transformed data and untransformed reports from the literature. In our study, data were not transformed before analysis. The univariate models for each lamb survival trait included the overall mean, fixed effects of birth year (9 levels: 1975 to 1983), birth type (3 levels: single, twin, or greater order multiple including 4 litters of quadruplets and 1 litter of quintuplets), flock (15 levels), sex (2 levels), and age of dam (6 levels: 2 to ≥7 yr), which were all significant factors in the earlier phenotypic analysis of these data (Hatcher et al., 2009). The random components included effects for direct genetic ($\boldsymbol{\sigma^2_d}$), maternal genetic ($\boldsymbol{\sigma^2_m}$), and maternal permanent environment ($\boldsymbol{\sigma^2_{pe}}$) effects and the covariance between additive and dam genetic variances ($\boldsymbol{\sigma_{dm}}$). The phenotypic variance was calculated as the sum of each of the variance components ($\sigma^2_p = \sigma^2_d + \sigma^2_m + \sigma^2_{pe} + \sigma_{dm} + \sigma^2_e$), where $\sigma^2_e$ is the error or remainder.

Estimates of the direct and maternal heritability were obtained by dividing the respective variance component by the phenotypic variance. The repeatability of ewe rearing ability was estimated as the proportion of phenotypic variation accounted for by direct genetic and maternal effects, their covariance, and the maternal permanent environment [$(\sigma^2_d + \sigma^2_m + \sigma_{dm} + \sigma^2_{pe})/\sigma^2_p$]. Phenotypic and genetic correlations between the various survival traits were estimated using a series of bivariate analyses. The appropriate covariance,

**Table 1.** Mean lamb survival and estimates of phenotypic variance ($\sigma^2_p$), additive direct genetic variance ($\sigma^2_d$), maternal genetic variance ($\sigma^2_m$), covariance ($\sigma_{dm}$), and dam permanent environmental variance ($\sigma^2_{pe}$)

| Trait | Mean | $\sigma^2_p$ | $\sigma^2_d$ | $\sigma^2_m$ | $\sigma_{dm}$[1] | $\sigma^2_{pe}$ |
|---|---|---|---|---|---|---|
| Survival within time periods | | | | | | |
| 1 to 7 d | 0.858 | 0.115 ± 0.001 | 0.002 ± 0.001 | 0.005 ± 0.002 | −0.001 ± 0.001 | 0.007 ± 0.002 |
| 7 to 110 d | 0.893 | 0.092 ± 0.001 | 0.005 ± 0.001 | 0.003 ± 0.001 | −0.002 ± 0.002 | 0.000 ± 0.001 |
| Cumulative survival from birth to | | | | | | |
| 1 d | 0.944 | 0.053 ± 0.001 | 0.002 ± 0.001 | 0.004 ± 0.001 | −0.002 ± 0.001 | 0.004 ± 0.001 |
| 7 d | 0.810 | 0.148 ± 0.002 | 0.004 ± 0.002 | 0.006 ± 0.002 | −0.002 ± 0.002 | 0.014 ± 0.002 |
| 30 d | 0.785 | 0.161 ± 0.002 | 0.003 ± 0.002 | 0.008 ± 0.003 | −0.002 ± 0.002 | 0.012 ± 0.002 |
| 110 d | 0.724 | 0.189 ± 0.002 | 0.005 ± 0.002 | 0.006 ± 0.003 | −0.001 ± 0.002 | 0.011 ± 0.002 |

[1]Covariance between additive and dam genetic variance ($\sigma_{dm}$) was not significant ($P > 0.05$).

phenotypic or genetic, between each pair of survival traits, x and y, was divided by the square root of the product of the phenotypic variance of each trait ($r_{xy} = \sigma_{xy}/\sqrt{(\sigma^2_x \cdot \sigma^2_y)}$). The maternal genetic and maternal permanent environment correlations were calculated in the same manner.

Variation in maternal bond score and lamb birth weight was partitioned using the same univariate model applied to the survival traits with the direct heritability, maternal heritability, and repeatability calculated from the variance components as described above. Phenotypic, genetic, maternal genetic, and maternal permanent environment correlations were estimated between maternal bond score, lamb birth weight, and each of the survival traits as outlined previously.

## RESULTS

### *Lamb Survival*

The largest variance component for cumulative survival and survival within time periods was the maternal permanent environment except for survival between 7 and 110 d (Table 1). For cumulative survival, the maternal permanent environment accounted for between 5.8 and 9.5% of the phenotypic variance, but there was no consistent trend with increasing lamb age. The maternal genetic variance was the next largest component with the direct genetic effects accounting for the smallest proportion of the observed variation. Survival within 1 to 7 d of age followed the same trend, but the direct genetic variance was greater than the direct maternal variance between 7 d of age and weaning. There was evidence of significant maternal permanent environmental variance up to 7 d, although it was effectively zero between 7 and 110 d. The significant cumulative maternal permanent environmental variance to 30 and 110 d was carried over from the early postnatal period. The covariance between direct and maternal effects was negative in both time periods and at all ages but not significantly different from zero. The amount of phenotypic variation accounted for by the direct, maternal, and maternal permanent environment components across all ages and time periods shows that selection on lamb survival will result in little genetic gain in the trait.

Some ewes repeatedly lose lambs in the early postnatal period leading to dam repeatabilities, ewe rearing ability, greater than 0.10 in the first week of life and the greatest repeatabilities for early cumulative survival at 1 and 7 d (Table 2). But repeatability in the later postnatal period (between 7 and 110 d) was about one-half that of the early postnatal period, indicating that beyond 7 d lamb survival is largely outside the control of the ewe.

The heritability of lamb survival was low for direct (0.02 to 0.05) and maternal genetic (0.03 to 0.07) effects (Table 2). Maternal heritability between 1 and 7 d was double that of the direct heritability, but the reverse occurred between 7 and 110 d when the direct heritability (0.05) was greater than the maternal heritability (0.03). For cumulative survival, the direct heri-

**Table 2.** Estimates of direct and maternal heritability and dam repeatability for lamb survival within each time period

| Trait | Direct heritability | Maternal heritability | Dam repeatability |
|---|---|---|---|
| Survival within time periods | | | |
| 1 to 7 d | 0.022 ± 0.010 | 0.045 ± 0.017 | 0.120 ± 0.011 |
| 7 to 110 d | 0.053 ± 0.014 | 0.029 ± 0.016 | 0.060 ± 0.013 |
| Cumulative survival from birth to | | | |
| 1 d | 0.035 ± 0.011 | 0.066 ± 0.018 | 0.140 ± 0.012 |
| 7 d | 0.028 ± 0.010 | 0.040 ± 0.017 | 0.147 ± 0.011 |
| 30 d | 0.020 ± 0.010 | 0.048 ± 0.017 | 0.129 ± 0.011 |
| 110 d | 0.027 ± 0.010 | 0.034 ± 0.015 | 0.110 ± 0.011 |

**Table 3.** Direct genetic (below diagonal) and phenotypic (above diagonal) correlations for cumulative lamb survival across time periods

| Cumulative survival to | 1 d | 7 d | 30 d | 110 d |
|---|---|---|---|---|
| 1 d | | 0.512 ± 0.006 | 0.475 ± 0.007 | 0.402 ± 0.007 |
| 7 d | 0.721 ± 0.164 | | nc[1] | 0.776 ± 0.003 |
| 30 d | 0.854 ± 0.192 | nc | | 0.841 ± 0.002 |
| 110 d | 0.487 ± 0.209 | 0.662 ± 0.136 | 0.749 ± 0.121 | |

[1]nc = The analysis did not converge for these pairs of estimates.

tability was consistently about a one-half to one-third less than the maternal heritability at all lamb ages with no consistent trend evident with increasing lamb age.

As expected, the phenotypic and genetic correlations for the direct genetic effect across time periods were all positive and high (Table 3) because of the part-whole nature of these relationships (i.e., only surviving lambs at the start of the preceding time period were considered for the subsequent one). This was also the case for maternal genetic and permanent environmental correlations (Table 4). The inability to estimate the correlation between cumulative lamb survival at 7 and 30 d was due to the large proportion of lambs surviving from 7 d to marking and has been reported previously (Cloete et al., 2009).

## *Maternal Bond Score*

The average maternal bond score was 1.8, indicating that on average the ewes tended to maintain reasonable contact with their lamb during the tagging, weighing, and scoring activities. The phenotypic variance was 0.46 ± 0.01 with the direct genetic, maternal genetic, and maternal permanent environment estimates each accounting for about 20% of the phenotypic variance (0.09 ± 0.01, 0.10 ± 0.02, and 0.09 ± 0.01, respectively; Table 5). The covariance between the direct and maternal genetic effects was −0.06 ± 0.01. Maternal bond score was a highly repeatable trait (0.49 ± 0.02) with moderate direct (0.20 ± 0.02) and maternal (0.23 ± 0.03) heritability. However, the phenotypic correlations between maternal bond score and lamb survival across ages were low. Although the corresponding genetic correlations were greater, they had large SE (Table 5). The maternal genetic and permanent environmental correlations with lamb survival at each age also had large SE.

## *Birth Weight*

The average birth weight of lambs in this study was 3.63 kg. The additive direct variance accounted for the majority (24%; 0.10 ± 0.01) of the phenotypic variance (0.42 ± 0.01) observed for lamb birth weight, followed by the maternal genetic (14.9%; 0.06 ± 0.01) and dam permanent environmental variance (9.7%; 0.04 ± 0.01). The covariance between the direct and maternal genetic effects was −0.03 ± 0.01. The dam repeatability of lamb birth weight was moderate (0.40 ± 0.02) with the direct heritability being greater than the maternal estimate (0.24 ± 0.02 vs. 0.15 ± 0.02, respectively). The phenotypic and genetic correlations between lamb birth weight and survival were positive but low for all ages (Table 5), and practically they were not significantly different to zero. The smallest phenotypic correlation was observed at birth (0.04) and smallest genetic correlation at 110 d (0.01). The maternal genetic correlation was also low at birth (0.08) but greater at the other lamb ages (0.39, 0.36, and 0.30 at 7, 30, and 110 d, respectively).

# DISCUSSION

Maternal genetic effects (ewe rearing ability) were more important than direct genetic effects (lamb viability) for cumulative lamb survival at birth, 7 d of age, marking and weaning, and for survival between 1 and 7 d of age of those lambs that survived birth. Whereas this result is consistent with earlier work using other breeds of sheep (Burfening, 1993; Lopez-Villalobos and

**Table 4.** Maternal genetic (below diagonal) and permanent environmental (above diagonal) correlations for cumulative lamb survival across time periods

| Cumulative survival to | 1 d | 7 d | 30 d | 110 d |
|---|---|---|---|---|
| 1 d | | 0.874 ± 0.074 | 0.518 ± 0.174 | 0.816 ± 0.099 |
| 7 d | 0.468 ± 0.192 | | nc[1] | 0.986 ± 0.032 |
| 30 d | 0.802 ± 0.084 | nc | | 0.997 ± 0.024 |
| 110 d | 0.559 ± 0.187 | 0.967 ± 0.063 | 0.971 ± 0.042 | |

[1]nc = The analysis did not converge for these pairs of estimates.

**Table 5.** Correlations between maternal bond score, lamb birth weight, and cumulative survival at birth (1 d) and to 7, 30, and 110 d of age

| Trait | 1 d | 7 d | 30 d | 110 d |
|---|---|---|---|---|
| Maternal bond score | | | | |
| Phenotypic | 0.087 ± 0.011 | 0.020 ± 0.010 | 0.012 ± 0.010 | 0.012 ± 0.010 |
| Genetic | −0.128 ± 0.151 | 0.122 ± 0.149 | 0.105 ± 0.175 | 0.161 ± 0.149 |
| Maternal genetic | −0.111 ± 0.188 | −0.061 ± 0.206 | −0.088 ± 0.191 | 0.008 ± 0.210 |
| Dam permanent environmental | 0.011 ± 0.104 | −0.040 ± 0.090 | −0.057 ± 0.097 | −0.132 ± 0.107 |
| Lamb birth weight | | | | |
| Phenotypic | 0.039 ± 0.009 | 0.141 ± 0.009 | 0.143 ± 0.009 | 0.129 ± 0.009 |
| Genetic | 0.064 ± 0.136 | 0.139 ± 0.136 | 0.098 ± 0.160 | 0.007 ± 0.140 |
| Maternal genetic | 0.085 ± 0.172 | 0.388 ± 0.177 | 0.359 ± 0.164 | 0.297 ± 0.185 |
| Dam permanent environmental | 0.171 ± 0.128 | 0.058 ± 0.114 | 0.132 ± 0.120 | 0.229 ± 0.129 |

Garrick, 1999; Sawalha et al., 2007; Maxa et al., 2009), few previous studies have further partitioned the maternal effects to separate the permanent environment component (Morris et al., 2000; Southey et al., 2001; Cloete et al., 2009). This is the first study to do so at more than 1 time period between birth and weaning.

At each lamb age the maternal permanent environment contributed more to the observed variation than the maternal genetic effect. Comparable results were identified by Morris et al. (2000) and Lopez-Villalobos and Garrick (1999) working with Romney sheep and Barwick et al. (1990) with the US Suffolk. This indicates that the permanent environmental component of the maternal effect is the main determinant of the repeatability of lamb survival. At birth, variation in the maternal permanent environment could be due to physiological differences between dams in their ability to provide nutrients to the developing fetus (Koch and Clark, 1955) and physical differences in pelvic dimensions (Haughey et al., 1985). In addition, behavioral changes at the onset of parturition have impacts on survival, including the ability of a ewe to separate herself from the mob, identify and occupy a birth site conducive to lamb survival, exhibit appropriate maternal behavior (Lindsay et al., 1990), cooperate with the first suckling attempts without aggressive behavior (Alexander, 1988; Cloete et al., 2002), and remain with her lamb(s) for 6 h (Murphy et al., 1994). After parturition it is likely that differences in colostrum production as well as the onset and duration of lactation would contribute to variation in the permanent maternal environment (Bradford, 1972).

Interestingly, the maternal permanent environment component for survival between 7 and 110 d of those lambs that were alive at 7 d of age was negligible. Within this time period the direct genetic variance accounted for the largest component of the observed phenotypic variation, indicating that the ability of the lamb to survive on its own is more important than the mothering ability of the ewe between 7 d of age and weaning. Therefore, after 7 d, milk production of the dam has little impact on survival, although it will obviously continue to impact on the growth and physiological development of her progeny.

The covariance or correlation between the direct and maternal effects at each lamb age and within each time period in this study, although negative, were essentially zero. Some previous studies (Burfening, 1993; Lopez-Villalobos and Garrick, 1999; Morris et al., 2000; Southey et al., 2001; Everett-Hincks et al., 2005) also report negative correlations between maternal and direct genetic effects on lamb survival, but of a greater magnitude. The conclusion from these studies was that improvements in one component of survival may be associated with reductions in the other, making overall genetic progress in lamb survival slow. Everett-Hincks et al. (2005) and Ch'ang and Rae (1972) proposed that lambs with superior survival to weaning have inferior genes for survival of their own progeny when they become mothers. However, other work (Barwick et al., 1990; Matos et al., 2000; Sawalha et al., 2007) reported positive correlations, albeit with large SE, which suggests that dams with good genetic mothering ability have better direct genetic potential to produce lambs with reduced mortality rate at birth. Variation between studies in the size of the data set and models used for analysis (Burfening, 1993) do have a significant impact on the accuracy of estimating covariance components and genetic parameters and care must be taken to ensure valid comparisons are made between studies. Breed differences may also play a role (Burfening, 1993; Matos et al., 2000; Maxa et al., 2009). Larger data sets are required to estimate the direct maternal correlation with sufficient precision to make conclusions about the biological nature of this relationship.

Dam repeatability is a measure of the likely response to selection that can be achieved in the current generation. At all lamb ages and for survival to 7 d of age of those that survived birth, ewe rearing ability had an estimated repeatability of at least 0.11, indicating that multiple records of the rearing ability of a ewe over its lifetime can increase selection accuracy. More importantly, such repeatabilities indicate that current generation improvement can be achieved by culling ewes with poor rearing ability from the breeding flock. However, the estimated repeatability decreased with increasing age of the lamb. For survival between 7 d and weaning of those lambs that survived their first week of life, the repeatability of rearing ability of the dam was about one-half that at all other time periods. This emphasizes the need to record survival as a trait of the dam within 7 d of birth to improve the accuracy for evaluation and selection purposes.

Heritability is a measure of future generation genetic response, so the very low heritabilities for lamb survival, less than 0.03, and for ewe rearing ability, 0.07, suggest that genetic solutions to increase lamb survival are unlikely to be significant. Similar estimates of direct and maternal heritability were reported by Safari et al. (2005b) for a range of breeds. But, despite the low heritabilities, there is still potential for improvement through selective breeding. Using assumed figures of 0.75 average survival rate, heritability of 0.08, repeatability of 0.12, and standardized selection differential of 1.3, potential rates of progress of 0.024 in mean survival per generation using a single record of the rearing ability of a ewe or 0.036 per generation using an average of 3 dam records are possible. Such genetic improvement rates would not be attained under practical situations because they refer to single trait selection using complete records on ewe rearing performance. However, these data do indicate that where a breeding program aims to increase reproductive efficiency, ewe rearing ability needs consideration. Of course, such attention would be more practical and economically beneficial if suitable indirect selection criteria for ewe rearing ability were available.

Hatcher et al. (2009) identified only small differences between the 15 Merino subflocks represented in the Trangie flock for survival at birth. Significant differences between the subflocks were evident for survival to 7 d of age and to weaning, but these were only substantial for twin-born lambs. To quantify the relative size of the between-flock and within-flock genetic variation, we have used overall survival from birth to weaning. The between-flock variance was 50 and 40% of the within-flock direct genetic and maternal genetic variances, respectively. So, despite the relatively low heritability of the trait, within-flock selection is still a more realistic avenue for improvement in lamb survival than selection among flocks.

The genetic and phenotypic correlations for lamb survival across time periods and the maternal genetic and permanent environment correlations were always positive. Survival to 7 d, marking, or weaning were all strongly correlated with each other. This indicates that genes controlling the direct, maternal, or permanent environment that favor early survival may also favor survival at later ages. However the size of the maternal effect decreases substantially once the lamb is 7 d old. These correlations are based on cumulative lamb survival, whereas correlations between independent time periods, if able to be estimated, are likely to remain positive but be less in magnitude.

This study has highlighted the need to discriminate between traits that may have some explanatory role in the variation between animals in survival compared with their potential roles as selection or management criteria. Maternal bond score, an assessment based on the movement of the ewe away from her lamb at tagging, has been incorporated with some (O'Connor et al., 1985) or little (Everett-Hincks et al., 2005) success into ewe selection and culling programs in New Zealand. Given the relative importance of ewe rearing ability compared with lamb viability, on early lamb survival in particular, maternal bond score would appear a likely selection criterion for improved lamb survival. However, in the present study, although maternal bond score was a highly repeatable and moderately heritable trait, the genetic and phenotypic correlations with lamb survival were essentially negligible. For this flock at least, maternal bond score was a very poor indirect selection criterion for ewe rearing ability. However, it must be remembered that in addition to assessing the attachment of a dam to her newborn lamb, maternal bond score also gauges ewe temperament, specifically her reaction to the presence of humans (Sawalha et al., 2007). If lamb tagging occurred within the 6 h window after birth before the ewe lamb bond is firmly established (Murphy et al., 1994), it is possible the reaction of the ewe to the human at tagging would be greater than the still forming bond with her lamb. This would be particularly true if the newborn lamb was lethargic and not actively contributing to the formation of the ewe-lamb bond (Lindsay et al., 1990).

Lamb birth weight was also highly repeatable and moderately heritable in agreement with previous work (Snyman et al., 1995; Al-Shorepy and Notter, 1998; Safari et al., 2005b, 2007; Riggio et al., 2008; Cloete et al., 2009). The genetic and phenotypic correlations between birth weight and lamb survival were low, particularly for survival to 1 d of age. This is not surprising given that at this age there is a curvilinear relationship between birth weight and lamb survival, with light and heavy lambs more likely to die (Hall et al., 1995; Morris et al., 2000; Sawalha et al., 2007; Hatcher et al., 2009). The phenotypic correlations were slightly greater for cumulative survival to older ages, but the genetic correlations were not significantly different from zero. It is possible that the phenotypic correlations reflect those light birth weight lambs that died due to starvation, mismothering, and exposure, which have no genetic basis. On the other hand, the genetic correlations reflect the heavier birth weight lambs that died due to dystocia, which has both a direct genetic basis (Smith, 1977) and possibly a maternal genetic component (Cloete et al., 2002). Therefore, like maternal bond score, lamb birth weight has limited potential as an indirect selection criterion for lamb survival.

The estimated genetic parameters for both lamb viability and ewe rearing ability suggest that genetic improvement in lamb survival will be very slow, but some opportunity exists to identify ewes that are more reliable in rearing their lambs. Survival in the later postnatal period (after 7 d) was less repeatable, which emphasizes the need to record survival within 7 d of birth to improve the accuracy of the trait for evaluation and selection purposes. The key is to identify appropriate selection criteria. Genetic variation in lamb survival has been confirmed as principally arising from genetic variation in ewe rearing ability. The exploitation of this variation, both within and between flocks, would be substantially improved by the identification of highly correlated indirect selection criteria. Unfortunately, no such criteria were identified in our study. Additionally, we need information on the genetic relationships between ewe rearing ability and other traits of commercial importance in the Australian Merino to better predict the likely outcome of breeding programs to increase profitability.

Events occurring in the early postnatal period are critical for lamb survival because most lamb deaths occur during this time (Hatcher et al., 2009). Although manipulation of ewe nutrition specifically to increase birth weight is unlikely to increase lamb survival (Hatcher et al., 2009), the ewe must have sufficient body reserves at parturition to facilitate a quick delivery, begin lactogenesis with an adequate quantity of colostrum, and provide satisfactory maternal care to her lamb. The lamb will benefit by having a greater amount of body reserves, particularly brown adipose fat, to metabolize postbirth (Vermorel and Vernet, 1985). Merino producers can facilitate this by ensuring the nutritional requirements of breeding ewes, particularly multiple-bearing ewes, are met during the later stages of pregnancy. Similarly provision of a suitable lambing environment that, first, encourages the ewe to choose a sensible birth site and remain there for at least 6 h and, second, moderates environmental conditions is likely to improve the chance of individual lambs surviving their first week of life.

The average survival to weaning in this study was 72.4%, which would have little impact on estimates of genetic parameters using observed or transformed data. The results of Safari et al. (2005a) confirmed that direct and maternal variances can be underestimated when using a logit-transformation and might give unexpected results. Survival rates at either end of the scale, less than 10% or greater then 90%, would require a logit-transformation. For studies with less or greater incidence of survival, threshold analysis methods may be useful. However, Matos et al. (2000) reported no significant differences in the predictive ability of linear and threshold models when analyzing lamb survival in Rambouillet and Finnsheep flocks. The survival rates in their study were comparable with this study, 81.9% for the Rambouillet and 75% for the Finnsheep. Therefore we considered the mixed model analysis procedure used in this study was adequate and had the added benefit of ease of interpretation of results.

Despite these data being recorded between 1975 and 1983, these results remain relevant to the present-day Australian sheep and wool industry. Recent studies of the genetics of lamb survival using data from Merino resource flocks in South Australia established in the late 1980s (Brien et al., 2009b) and preliminary results from the Cooperative Research Centre for Sheep Industry Innovation's Information Nucleus flock established in 2007 (Brien et al., 2009a) use similar methods of analyses and report genetic parameters similar to those in this study.

## LITERATURE CITED

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