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Genetics of lamb survival

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ABSTRACT

Data from seven commercial New Zealand sheep flocks were analysed to quantify the extent to which lamb survival in New Zealand sheep is influenced by genetic factors. Estimates of direct and maternal genetic variance components, and the effects of inbreeding in either the lamb or the dam on lamb survival, were found to vary significantly across flocks. Direct heritability estimates ranged from 0.008 to 0.070, while maternal heritability estimates ranged from 0.002 to 0.075. Inbreeding in the lamb showed a statistically significant ($P < 0.05$) effect on survival in three of the seven flocks, ranging in value from -0.17 to -0.29% reduction in lamb survival for a 1% increase in inbreeding coefficient. Inbreeding of the lamb's dam had a statistically significant effect ($P < 0.05$) on survival in two of the seven flocks, taking values of -0.32 to -0.71% reduction in lamb survival for a 1% increase in the dam's inbreeding coefficient. It is recommended that lamb survival records be transformed to a constant variance within flock and year prior to estimation of breeding values, but that no transformation to either a logit or probit scale within the statistical analysis is required. Inbreeding coefficients for both the lamb and the lamb's dam should be included as linear covariates in the mixed-model analysis of lamb survival breeding values.

Keywords: Lamb survival; inbreeding; sheep; estimated breeding value; heritability.

INTRODUCTION

While lamb survival is a trait of high economic importance in sheep genetic selection (Amer *et al.*, 1998), there are many complexities associated with the estimation of breeding values for lamb survival. For example, lamb survival is a binomially distributed trait (i.e., each animal either survives or dies with no intermediates), and it is affected by the maternal performance of a lamb's dam, in addition to the genes inherited from both sire and dam (Lopez-Villalobos & Garrick, 1999). Lamb survival is also known to be affected by inbreeding, both in the lamb itself, and in its mother (Lamberson & Thomas, 1984).

The objectives of this study were to estimate the extent of genetic effects (including inbreeding) on lamb survival, using data from New Zealand recorded sheep flocks. Implications for genetic evaluation within New Zealand sheep populations are discussed.

MATERIAL AND METHODS

Data

Data from seven New Zealand sheep flocks were used. The characteristics of the data and flocks are summarised in Table 1. One composite flock (with a terminal-sire selection emphasis) was considered, while the remaining

six flocks were made up of dual-purpose sheep, with a substantial proportion of lambs born as multiples. Lamb survival, coded as zero for animals dying prior to weaning and 1 otherwise, was taken as the trait of interest.

A number of years of data were omitted from the analyses. To save the time involved in tracking down specific errors, all years of lamb survival records prior to and including the latest year that any data anomaly was identified, was omitted from consideration. For example, an absence or very low number of dead lambs recorded for the year, or a sire within a year, resulted in all lamb survival records up to and including that year being omitted. However, all available pedigree information was retained. No attempt was made to account for breed importations to the imported flocks, or for breed component in the composite flock.

Statistical methods

Estimates of fixed and random effects on lamb survival records were made using ASREML (Gilmour *et al.*, 1999). Analyses were first carried out assuming that lamb survival was normally distributed. Subsequent analyses considered the effects of using probit and logit transformations of lamb survival within the statistical procedures applied. Birth rank, age of dam, flock of birth

TABLE 1: Summary of flock and data characteristics for seven flocks used to estimate genetic and phenotypic variance components and inbreeding effects for lamb survival.

	Flock 1	Flock 2	Flock 3	Flock 4	Flock 5	Flock 6	Flock 7
Breed ¹	Rom	Coop	Rom	Rom	Coop	Comp	Rom
Average lamb survival %	83	88	90	92	92	89	90
Ave lambs born per year	2500	1400	2200	5000	1000	2000	9000
% lambs coded born dead	12	8	7	4	7	7	7
% lambs coded died later	5	4	Variable	0	1	4	3
No. years survival records used	18	12	10	26	10	6	5
No. years of pedigree used	26	18	29	32	22	14	33
% lambs born as singles	15	13	10	17	10	20	14

¹Rom = Romney, Coop = Coopworth, Comp = composite

TABLE 2: Summary of estimated variance component ratios and phenotypic variance for lamb survival analysed assuming records are normally distributed

	Flock 1	Flock 2	Flock 3	Flock 4	Flock 5	Flock 6	Flock 7
Heritability (direct)	0.070	0.010	0.022	0.038	0.008	0.013	0.014
Standard error	0.010	0.006	0.007	0.003	0.007	0.008	0.004
Heritability (maternal)	0.016	0.002	0.009	0.075	0.002	0.013	0.024
Standard error	0.005	0.005	0.006	0.006	0.005	0.009	0.006
Maternal environment	0.058	0.062	0.084	0.146	0.062	0.152	0.167
Standard error	0.005	0.008	0.008	0.006	0.008	0.012	0.008
Phenotypic variance ¹	0.132	0.108	0.103	0.097	0.078	0.098	0.094

¹The phenotypic variance is expressed on the observed 0/1 scale (i.e. not percent scale)

(when subsets of a breeding flock were managed on more than one property), year of birth, and inbreeding coefficient for the lamb were considered as fixed effects, and fitted for all models and on all data sets, irrespective of whether or not they were found to be statistically significant. Age of maternal granddam, as well as birth rank and inbreeding coefficient each for the lamb's dam were also considered as fixed effects for all models and data sets. Random effects included direct and maternal genetic effects (assumed to be uncorrelated with each other), and permanent environmental effects of each dam over her lifetime. Both the inclusion of statistically significant interactions among fixed effects, and the omission of statistically non-significant fixed effects were found to have trivial effects on variance component estimates in trial analyses. Inbreeding coefficients were calculated using all available pedigree information and fitted as linear covariates after no significant quadratic effects of inbreeding were found.

To further test for trends and consistency in variance component estimates, Flocks 1 to 5 were broken up into subsets of the two most recent five-year periods and the analyses repeated.

RESULTS

Table 2 shows the estimates of random effects across the seven flocks when lamb survival was assumed to be a normally distributed trait. Flock 1, which had the highest direct heritability, showed a much lower heritability (0.029 and 0.021 vs 0.070) when estimated using the two most recent five-year sub-sets of the data. If a direct heritability estimate of 0.025 is taken for Flock 1, then the average over the seven flocks was reduced from 0.025 to 0.019. Also, Flock 4, which had the highest maternal heritability, showed a much lower value in the most recent five years of data (0.018 vs 0.075). If a maternal heritability estimate of 0.018 is taken for Flock 4, then the average over the seven flocks was reduced from 0.020 to 0.012. Maternal permanent environmental effects accounted for substantially more of the variance in the data than either direct or maternal genetic effects (Table 2).

For direct estimates of heritability, average (over all seven flocks) estimates using logit and probit transformations were lower by 0.001 and 0.013 compared with values in Table 2 (individual flock results not shown). Maternal genetic heritability estimates were higher by 0.016 and 0.007 respectively. Permanent maternal

environmental effects were higher by 0.020 and by 0.007 respectively. In comparison to the differences in variance component estimates observed across the different flocks both with and without the transformations, these differences in average levels are quite low.

Table 3 summarises the effects of inbreeding on lamb survival in Flocks 1 to 3 estimated assuming lamb survival is a normally distributed trait. After appropriate back transformation to the observed scale, estimates using probit and logit transformation models were found to be very similar (results not shown). No significant effects of inbreeding in the lamb or dam were found in Flocks 4 to 7, irrespective of whether or not a transformation was applied. In Flocks 5 to 7, animals with inbreeding coefficients greater than 5% were very uncommon.

TABLE 3: Summary of lamb and dam inbreeding on lamb survival (% per %) in Flocks 1 to 3.¹

	Flock 1	Flock 2	Flock 3
Lamb inbreeding effect	-0.27	-0.29	-0.17
(Standard error)	(0.08)	(0.17)	(0.09)
Dam inbreeding effect	0	-0.71	-0.32
(Standard error)	0	(0.21)	(0.12)

¹Estimates of inbreeding effects on lamb survival for Flocks 4 to 7 were not significantly different from zero and so are not shown.

Estimates of fixed effects (other than inbreeding) are not shown here as there were many estimates and they were consistent with expected values (e.g., Nicoll *et al.*, 1999).

DISCUSSION

On average, the estimates of direct and maternal genetic variance components for lamb survival described here were higher than the values reported for a single flock by Lopez-Villalobos & Garrick (1999). However, a very strong feature of the results was the variability in genetic parameter estimates across flocks. Some of this variability may be attributed to sampling error, although true differences in the underlying genetic parameters seems likely. It is difficult to speculate on the cause of this variability, although differences in frequency of unfavourable recessive genes affecting lamb survival across flocks is one potential contributing factor. Substantial differences in the estimates of lamb inbreeding effects are also consistent with this explanation. However, differences among flocks in the accuracy of parentage

identification of live and/or dead lambs could also explain this.

The high permanent maternal environmental effects relative to maternal genetic effects, suggests that culling of ewes based on their lamb survival records could be very inefficient from the perspective of increasing genetic merit of the flock. Similarly, some breeders only select breeding rams mothered by ewes with a good lamb survival record. Under this practice, some very good rams may be inappropriately excluded from consideration. In contrast, a high maternal permanent environment effect suggests that culling commercial flock ewes after losing lambs over several lambings could significantly improve lamb survival in the commercial flock. Further work is needed to quantify this. Lack of a practical method of identifying ewes that lost lambs in successive seasons could be a further limitation to the application of this type of culling in a commercial flock.

The estimates of effects of inbreeding in the lamb, and in its dam, were both found to be lower than the averages of published estimates reported by Lamberson & Thomas (1984). An increase in inbreeding in the lamb by 1% resulted in increases in the lamb death rate by 0.17% to 0.29% (excluding those flocks with no significant effect). A value of 0.2% would imply that lambs from sire-daughter or full-sib matings would have 5% lower survival when compared to non-inbred lambs. Alternatively, a flock in which inbreeding had increased to the extent where the average inbreeding coefficient of lambs born was 5%, then taking a value of 0.2 implies that survival would be 1% lower than a non-inbred flock.

If a 1% increase in the inbreeding coefficient of a lamb's mother resulted in a 0.5% increase in lamb death (estimates were 0.71% and 0.32% in two of the seven flocks only) it would be expected that ewes resulting from sire-daughter or full-sib matings would have lamb survival lower by 12.5% compared to lambs out of non-inbred ewes. Alternatively, a flock in which inbreeding had increased to the extent where the average inbreeding coefficient of ewes was 5%, then taking a value of 0.5 implies that survival would be 2.5% lower than a non-inbred flock.

The results of this study suggest that routine analyses of lamb survival would not require computationally expensive transformations to a logit or probit scale. However, maternal genetic effects should be estimated simultaneously with direct genetic effects, and data should be rescaled to a standard phenotypic variance as the variance of a binomial trait is closely linked to the mean incidence. Failure to standardise the variance would result in, for example, sires with progeny born in years of low average lamb survival having more widely spread lamb survival estimated breeding values than sires with progeny born in years with good average survival. Inbreeding coefficients for each recorded animal and its dam should be fitted as linear covariates, because there can be substantial differences in numbers of inbred progeny across sires within a flock. Detrimental effects of inbreeding on lamb survival disappear in animals bred to unrelated mates.

Because the heritability estimates were quite low, and

because dead lambs are effectively selected against automatically, economically significant variability in lamb survival breeding values is most common in sires with large numbers of progeny. Maternal breeding values for lamb survival are most variable and most accurate in sires with large numbers of daughters with lambing records.

Despite the low heritabilities, the amount of genetic variation in lamb survival remains high. For example, taking the direct heritability of lamb survival as 0.02, and assuming lamb survival averages 87%, the genetic standard deviation would be approximately 5%. In other words, two rams differing in their true breeding values by two genetic standard deviations would be expected to have a 5% difference in the survival of their progeny (remember that only one half of the lambs genes come from the sire). If each ram sires 500 progeny in his lifetime, 25 extra lambs would be lost from one ram. If a dead lamb constitutes a loss in profit of \$40 to the farm, then the cost of the lower survival would be \$1000 over the ram's working life.

In conclusion, despite low heritabilities, and apparent inconsistencies across flocks, sires with large numbers of progeny, and daughters with progeny, are expected to vary significantly in their estimated breeding values for direct and maternal lamb survival respectively. Routine systems that are robust to the many inherent problems associated with genetically evaluating lamb survival records will make a valuable contribution to New Zealand sheep breeding. This study has contributed to the development of such systems.

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