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Genetic parameter estimates for lamb survival in Romney sheep

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ABSTRACT

Lamb survival is a trait of economic importance in sheep production. Losses may be attributed to the lamb or to the behaviour of the dam. Maternal effects are environmental for the offspring but are at least partly genetic for the dam. The genetic evaluation of survival is complicated by the fact that this trait has a binomial distribution whereas most analytical procedures assume normality.

The objective of this study was to estimate heritabilities and genetic correlations for direct and maternal genetic effects using two underlying scales (probit and logit) for lamb survival in order to implement a new procedure of genetic evaluation.

Variance components were obtained by Restricted Maximum Likelihood (REML) procedures after transformation of the data using a linear mixed model. Records of survival were from 25,874 lambs born over the period 1989 to 1995 in a prolific Romney flock representing the progeny of 218 sires and 6,771 dams. The model included fixed effects of sex, year, litter size at birth and age of dam and the random effects for direct genetic, maternal genetic and maternal environmental influences.

Lambing and survival-to-weaning percentages were 178% and 87%, respectively. The estimates of heritability on the logit scale were 0.01, 0.03 and 0.04 for direct, maternal and total genetic effects, respectively. The proportion of total variance explained by maternal environmental influences was 0.09. The estimated genetic correlation between direct and maternal genetic effects was -0.26 . Similar estimates were obtained on the probit scale. Estimates will be lower for the observed scale.

These results indicate a greater opportunity for improving survival by manipulating the environment rather than by selection. However survival analysis is an important component of quality assurance in a genetic improvement scheme even if the resultant breeding values are not used for direct selection.

Keywords: Binomial distribution; heritability; maternal effects; lamb survival.

INTRODUCTION

Lamb survival to weaning is a major factor determining productivity of ewes (Dalton and Rae, 1978). Lamb survival in New Zealand is reported at 75 to 97% (Hight and Jury, 1970; Dalton *et al.*, 1980; Gumbrell and Saville, 1986). Lamb survival is a complex trait influenced by the individual capacity of the lamb to survive and by the rearing ability of the dam (Cundiff *et al.*, 1982; Piper *et al.*, 1982). The direct effect is due to the genes of the lamb affecting its own survival. Maternal effects are environmental for the offspring, but can have both genetic and environmental components for the dam (Bradford, 1972). Estimates of direct and maternal genetic effects and maternal permanent effects would be required if lamb survival is affected by the genetic merit of the individual and of the dam.

There is evidence of a small degree of genetic variation for survival from birth to weaning in sheep (Cundiff *et al.*, 1982; Piper *et al.*, 1982). Estimates of heritability for lamb survival average 0.04 as a trait of the lamb and 0.08 as a trait of the ewe (Cundiff *et al.*, 1982). Few studies (Barwick *et al.*, 1990; Burfening, 1993) have reported estimates of heritability for direct and maternal genetic effects for lamb survival.

Inbreeding causes a lower lamb survival (Lamberson and Thomas, 1984) whereas crossbreeding increases lamb survival (Nitter, 1978). However, the effects of heterosis are small and act principally on the direct component (Long *et al.*, 1989).

Estimation of variance components through mixed model methodology typically assumes that traits are continuous and normally distributed. Lamb survival has a binomial distribution and therefore variances and means are not independent (Lush *et al.*, 1948). An alternative is to assume there is an underlying scale (Lush *et al.*, 1948); individuals are scored 1 if they exceed a certain threshold value t , otherwise are scored 0. Mixed model methodology has been developed to estimate variance components for categorical traits assuming an underlying scale (Gilmour *et al.*, 1985; Im and Gianola, 1988). In this study, a model considering direct and maternal effects was used to estimate genetic parameters for lamb survival for an underlying scale using logit or probit models.

METHODS

Records from 25,874 lambs born over the period 1989 to 1995 in a prolific Romney flock were obtained from the national sheep data base. Information available was animal, sire and dam identification, year of birth, age of dam, and litter size in which the lamb was born. Lambing was recorded by daily shepherding with dead lambs recorded but without detail as to their sex. Lambs surviving to weaning were coded 1 whereas lamb not present at weaning were coded 0. Accordingly, survival included perinatal and tagging-to-weaning periods. Sex is known to affect lamb survival (Knight *et al.*, 1988) but in accord with industry practice, was not recorded on lambs found dead at tagging. Including three sexes (male, female, and unknown)

in the analysis was not appropriate as unknown sex animals had zero survival. Accordingly, for the purpose of estimating variance components, the sex of lambs found dead was assigned at random with equal probability for each sex.

The lambs were the progeny of 218 sires and 6,771 dams. Most sires were home bred but some outside sires were introduced. A total of 284 maternal grand sires were represented. A description of the data set is given in Table 1.

Ewes were not ultrasonically diagnosed for litter size (most carried multiples). No details were available to identify contemporary ewes in the same mob or paddock at lambing.

Variance components were obtained by Restricted Maximum Likelihood (REML) procedures after logit or probit transformation of the data with a linear mixed model using ASREML (Gilmour *et al.*, 1998). The model included fixed effects of sex, year of birth, litter size at birth and age of dam and the random effects for direct genetic, maternal genetic and maternal environmental influences.

TABLE 1: Description of the data set for lamb survival analysis.

Total records (lambs born dead or alive)	25,874
Number of litters	14,559
Number of dams	6,771
Number of sires	218
Number of maternal grand sires	284
Average litter size at birth	1.78
Average litter size at weaning	1.49
Average survival rate	87 %
Lambing percentage	178 %

RESULTS

Lambing and survival-to-weaning percentages were 178% and 87%, respectively (Table 1). All fixed effects were significant ($P < 0.01$) except sex effects but females had slightly higher survival than males (Table 2). Survival percentages varied across years reflecting the considerable effect of prevalent climate conditions on the survival of lambs. Twin lambs had higher survival than lambs born in litters of size 1, 3 and 4. Lambs born from mature ewes (3 to 5 yr old) had higher survival than lambs born from first lambing and aged ewes.

Estimates of genetic parameters for lamb survival are shown in Table 3. The estimates of heritability on the logit scale were 0.01, 0.03 and 0.04 for direct, maternal and total genetic effects, respectively. The proportion of total variance explained by maternal environmental influences was 0.09. The estimated genetic correlation between direct and maternal genetic effects was -0.26 . Similar estimates were obtained on the probit scale.

TABLE 2: Lamb survival for sex, year of birth, litter size, and dam age.

Effect	Number of lambs	Survival (%)
Sex		*
Male	12,900	86.5
Female	12,974	87.4
Year		**
1989	3,321	89.2
1990	3,757	87.5
1991	3,983	90.1
1992	3,865	76.4
1993	3,669	86.8
1994	3,602	89.5
1995	3,677	89.7
Litter size		**
1	4,233	85.1
2	18,568	89.0
3	3,021	77.3
4	52	65.4
Dam age		**
2	8,935	85.6
3	6,416	88.6
4	4,392	88.0
5	2,810	89.1
6	1,393	85.6
7	964	82.5
8	637	86.7
9	327	82.0

** $P < 0.01$; * $P < 0.05$

TABLE 3: Estimates of variance components and genetic parameters for lamb survival.

		Scale	
		Logit	Probit
Maternal permanent environmental variance	σ_{per}^2	0.353 \pm 0.07	0.086 \pm 0.02
Variance for direct genetic effect	σ_a^2	0.048 \pm 0.03	0.008 \pm 0.01
Covariance between direct and maternal	σ_{am}	-0.021 \pm 0.04	-0.004 \pm 0.01
Maternal genetic variance	σ_m^2	0.134 \pm 0.06	0.041 \pm 0.02
Residual variance	σ_e^2	3.290	1.000
Total variance	σ_p^2	3.803	1.131
Heritability for direct genetic effect	h_a^2	0.013 \pm 0.01	0.007 \pm 0.01
Heritability for maternal genetic effect	h_m^2	0.035 \pm 0.02	0.036 \pm 0.02
Total heritability	h_T^2	0.042 \pm 0.01	0.040 \pm 0.02
Genetic correlation between direct and maternal genetic effects	r_g	-0.257 \pm 0.41	-0.227 \pm 0.48

DISCUSSION

Average lamb survival of 87% found in this study agrees well with the range reported in other commercial flocks (Hight and Jury, 1970; Dalton *et al.*, 1980; Gumbrell and Saville, 1986).

Effects of sex on lamb survival reported in the literature indicates that males had lower survival rate than females (Hight and Jury, 1970; Dalton *et al.*, 1980; Petersson and Danell, 1985; Knight *et al.*, 1988) or that males and females have similar survival rate (Atkins, 1980). In the present study, sex effects on lamb survival were significant at $P < 0.05$ but not at $P < 0.01$. However, lambs that were found dead at tagging had not sex recorded. Accordingly, sex influences on survival need cautious interpretation.

Variation of lamb survival across years was considerable. Lamb survival ranged from 76 to 90%. Large variations were also reported by Hight and Jury (1970) and Knight *et al.*, (1988). Year effects account for variation in climatic conditions which affect lamb survival through the effects on the nutritional status of the grazing ewe and lamb (Donnelly, 1984).

A common observation is that very young ewes have lower lamb survival than older ewes (Hight and Jury, 1970; Atkins, 1980; Petersson and Danell, 1985; Knight *et al.*, 1988). Usually, the highest lamb survival rate is found for 4 to 6 year old dams (Knight *et al.*, 1988). This trend was observed in the present study (Table 2).

Some studies in New Zealand (Knight *et al.*, 1988) report that single-born lambs had higher survival than twin-born lambs. Others studies (Petersson and Danell, 1985) reported that survival rate of single-born lambs is lower than twin-born lambs but survival rate is reduced dramatically when litter size exceeds two lambs. This trend was observed in this study (Table 2). Bradford (1972) pointed out that litter size does not affect lamb survival directly but through its effects on birth weight. Birth weight strongly affect lamb survival and the relationship is curvilinear. This relationship was confirmed by Atkins (1980) and Knight *et al.*, (1988).

Despite the fact that estimates of heritability for lamb survival reported in the literature are low (Cundiff *et al.*, 1982; Piper *et al.*, 1982), a few studies have shown that lamb survival can be genetically improved, either by selecting rams based on their progeny survival (Knight *et al.*, 1979) or by selecting ewes on their rearing ability (Donnelly, 1982; Haughey, 1983; Cloete and Scholtz, 1998).

Estimates of heritability for direct and maternal effects of lamb survival obtained in this study using the underlying (logit or probit) scale are low (Table 3). Barwick *et al.*, (1990) reported estimates of heritability for direct and maternal genetic effects for lamb survival in the Suffolk breed of 0.025 and 0.017, respectively, on the observed scale. Estimates of heritability for lamb survival in the Targhee, Columbia and Rambouillet breeds were reported by Burfening (1993). The estimates ranged from 0.002 to 0.006 for direct effects and from 0.023 to 0.052 for maternal genetic effects. There is a close agreement between the results obtained in this study and those reported in the literature in spite of using the logit and probit transformation.

The proportion of total variance for lamb survival explained by maternal environmental of 0.09 (Table 3) agrees well with the value of 0.095 reported by Barwick *et al.*, (1990). The proportion of total variance explained by maternal environmental component was larger than the total (direct and maternal) genetic component. This indicates that the environmental component of the maternal effect is the main determinant of the repeatability of lamb survival viewed as a trait of the dam as reported by Morris *et al.*, (1996).

Estimates of genetic correlation between direct and maternal effects for lamb survival differ between studies. Estimates reported by Burfening (1993) ranged from -1.04 to 0.83 in the observed scale and Barwick *et al.*, (1990)

reported a value of 0.10 in the observed scale. The values of -0.26 and -0.23 in the logit and probit scale, respectively, estimated in this study suggest that improvement in one component of survival may be associated with reductions in the other component depending on the selection approach used.

CONCLUSIONS

The results obtained in the present study indicate a greater opportunity for improving survival by manipulating the environment rather than by selection. However survival analysis is an important component of quality assurance in a genetic improvement scheme. In developing schemes for genetic evaluation of animals for lamb survival, the negative genetic correlation between the direct and maternal genetic components should be taken into account.

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