Genetic parameters for lamb birth weight, survival and death risk traits

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ABSTRACT: This paper reports genetic parameters for lamb survival and mortality traits on sheep farms in New Zealand. Lamb survival and mortality records were obtained from 38 flocks (103,357 lambs) from 5 yr of lambing data (2007 to 2011) and include many breeds and their crosses (predominantly Romney, Perendale, Coopworth, and Texel). A number of models were tested, all including environmental weather effects and investigating the random environmental effect of dam and litter (dam/year) as well as logit transformation for binary traits. Total heritability (direct + maternal) estimates were low for lamb viability at birth (0.01), lamb death risk to dystocia (0.01), and lamb death risk to starvation exposure (0.01) from birth to 3 d of age in an analysis accounting for direct and maternal genetic effects and the maternal environmental effects. Lamb survival heritabilities reported are very low (total heritabilities range from 0.02 to 0.06). The total heritabilities for the lamb death risk traits are lower than reported estimates of survival to 3 d of age or to weaning suggesting selection for the postmortem traits are not warranted at this time within these flocks. The total heritability for lamb birth weight was moderate (0.38) and the genetic correlations with the lamb death risk traits suggested that directional selection on lamb birth weight would have an effect on survival, although it is likely to have a nonlinear effect and therefore an optimum birth weight at which survival is maximized. This study has also shown that the total heritabilities may be overestimated when not accounting for maternal genetic and environment effects and in particular not accounting for the random environmental effect of litter (dam/year).

Key words: birth weight, heritability, lamb death risks, lamb survival

INTRODUCTION

Farmers are seeking management practices and animal genetics to improve lamb survival. Many studies report low genetic variation for lamb survival to weaning suggesting that the scope for genetic selection to improve this trait is limited as it is under minimal genetic control (Hall et al., 1995; Lopez-Villalobos and Garrick, 1999; Morris et al., 2000; Everett-Hincks et al., 2005; Safari et al., 2005; Brien et al., 2010). Lamb survival is a complex trait influenced by direct genetic, maternal genetic, and environmental effects. The trait is observed over several months, from day of birth to weaning, with temporary environmental effects making up nearly 90% of the variation in lamb survival (Everett-Hincks et al., 2005). Numerous environmental factors, including weather and stock management practices, influence lamb survival over this period and could explain why previously reported estimates for the heritability of lamb survival have been low and genetic improvement limited. This has prompted a review of how the lamb survival trait is currently recorded (Everett-Hincks et al., 2005) and analyzed (Southey et al., 2001, 2003; Damgaard and Korsgaard, 2006). Studies by Southey’s team have reported higher heritability estimates when lamb mortality was analyzed using a competing risks approach (Southey et al., 2002) from using the actual age of lamb mortality (Southey et al., 2001, 2003).

This paper summarizes an investigation into the genetic effects on lamb survival and mortality traits on easy care sheep farms in New Zealand. We investigate the use of different models to calculate genetic parameters for lamb survival traits, calculated from industry data. It is intended that these estimates will be implemented into New Zealand’s genetic evaluation service (Sheep Improvement Limited [SIL], Dunedin,
New Zealand) to improve the accuracy of prediction of breeding values and thus enable the design of practical animal breeding programs representative of industry to reduce lamb mortality rates.

**MATERIALS AND METHODS**

Animal Ethics Committee approval was not sought for this study because the data were obtained from an existing database. Animal performance records were obtained from the AgResearch Lamb Survival Database and from the national sheep recording database, SIL, for 38 flocks (103,357 lambs) and for 5 yr of lambing data (2007 to 2011). The flocks included a range of breeds (36% Romney, 7% Perendale, 4% Coopworth, and 2% Texel) and their crosses (2 breed combinations; 11%) and composites (defined as a combination of 3 or more breeds; 35%; Price, 2000). This resource was used to estimate genetic parameters for the lamb traits described in Table 1 and to investigate management and environmental effects for these traits as previously reported in Everett-Hincks and Dodds (2008) and updated for this dataset (Table 2).

The flocks are part of the Ovita Lamb Survival research program and were performance recorded. All lambs that died between birth and 3 d of age were collected, tagged, and weighed and a postmortem was performed to determine cause of death. The postmortem examination procedure was modified from that described by McFarlane (1965), in consultation with veterinary practitioners, and is described by Everett-Hincks and Duncan (2008). The postmortem procedure first diagnosed lamb viability at birth (LVB) based on the presence of lung aeration and then assigned a primary cause of death, which included dystocia (lamb death risk from dystocia [LDD]; organ rupture, hemorrhage, or moderate to severe localized subcutaneous edema on head, neck, brisket, or rib cage), starvation exposure (lamb death risk from starvation exposure complex [LDSE]; no brown adipose tissue on heart and kidneys and no food in the gastrointestinal tract), and other causes (infection, congenital abnormality, other, or unknown). The study by Kerslake et al. (2005) characterized “primary dystocia” as localized moderate to severe (>3 mm thickness) subcutaneous edema on the lamb’s body at postmortem. The component traits are defined in Table 1.

Data were edited to remove missing records and small subclasses. Dams at least 2 yr of age were included, with dams older than 6 yr grouped with age group 6. Data collected on lambs from litters greater than 3 were removed from the dataset. Data collected on lambs that were fostered, hand reared, aborted, or resulted from embryo transfer or where their dam was assisted with lambing by the shepherd were also removed from the dataset.

Weather conditions, collected from the nearest weather station, were fitted in the analyses in the form of a sheep heat loss calculation described by Coronato (1999) used to describe environmental weather conditions. In this study, sheep heat loss values ranged from a minimum of 11 W/m² to a maximum of 108 W/m² with a mean of 47 W/m². Heat loss variables, calculated according to flock and date of lambing, were average heat loss 2 wk before birth, average heat loss 1 wk before birth, average heat loss on day of birth, and average heat loss 3 d from birth.

A pedigree file containing the sire, dam, and paternal and maternal grandparents of each animal born from 2001 was used to form a relationship matrix. The lambs were the progeny of 3,680 sires and 115,364 dams and there were 953 paternal grand sires, 1,642 paternal grand dams, 2,775 maternal grand sires, and 39,229 maternal grand dams. Heritabilities and correlations were calculated from variances and covariances estimated by use of ASReml (Gilmour et al., 2008).

Separate analyses were performed for all traits where the fixed effects and covariates tested remained
constant (Table 2); however, the following random effects were tested and differed between models:

1. **DMc**: direct additive genetic effect (D) + maternal genetic effect (M) + covariance between D and M,
2. **DMcL**: D + M + covariance between D and M + temporary environmental effect of dam/year,
3. **DMDam**: D + M + permanent environmental effect of dam, and
4. **DMLitter**: D + M + temporary environmental effect of dam/year.

The following traits were recorded as binary traits: LVB, LDD, LDSE, lamb survival to 3 d after birth (LS3d), and lamb survival to weaning (LSWWT) and were analyzed as normally distributed traits using the above models except for lamb survival to 3 d after birth (LS3d) and lamb survival to weaning (LSWWT) which were logit transformed. 

- **Number of records**
  - LBW: 103,537
  - LVB: 75,408
  - LDD: 73,660
  - LDSE: 73,694
  - LS3d: 97,424
  - LSWWT: 97,424

- **Trait mean ± RSD, kg**
  - LBW: 4.85 ± 0.577
  - LVB: 0.98 ± 0.140
  - LDD: 0.02 ± 0.139
  - LDSE: 0.02 ± 0.124
  - LS3d: 0.92 ± 0.244
  - LSWWT: 0.88 ± 0.285

**Fixed effects**

- **Flock**
- **Year of birth**
- **Litter size at birth**
- **Flock × year of birth**
- **Flock × litter size**
- **Year of birth × litter size**
- **Flock × year of birth × litter size**
- **Dam age**
- **Litter size × dam age**
- **Lamb sex**

**Covariates**

- **Date of birth**
- **Date of birth within flock within year of birth**
- **Average heat loss 2 wk before birth**
- **Average heat loss 1 wk before birth**
- **Average heat loss on d of birth**
- **Average heat loss 3 d from birth**

**Table 2. Final model effects for lamb traits recorded between birth and 3 d of age and survival to weaning age using the DMLitter random effects model**

| Lamb trait | LBW | LVB | LDD | LDSE | LS3d | LSWWT |
|------------|-----|-----|-----|------|------|-------|
| Number of records | 103,537 | 75,408 | 73,660 | 73,694 | 97,424 | 97,424 |
| Trait mean ± RSD, kg | 4.85 ± 0.577 | 0.98 ± 0.140 | 0.02 ± 0.139 | 0.02 ± 0.124 | 0.92 ± 0.244 | 0.88 ± 0.285 |

**Fixed effects**

- **Flock**
- **Year of birth**
- **Litter size at birth**
- **Flock × year of birth**
- **Flock × litter size**
- **Year of birth × litter size**
- **Flock × year of birth × litter size**
- **Dam age**
- **Litter size × dam age**
- **Lamb sex**

**Covariates**

- **Date of birth**
- **Date of birth within flock within year of birth**
- **Average heat loss 2 wk before birth**
- **Average heat loss 1 wk before birth**
- **Average heat loss on d of birth**
- **Average heat loss 3 d from birth**

1. **DMLitter** = random effects fitted include direct additive genetic effect + maternal genetic effect + temporary environmental effect of dam/year.
2. **LBW** = lamb birth weight (kg); **LVB** = lamb viability at birth (proportion); **LDD** = lamb death risk from dystocia (proportion); **LDSE** = lamb death risk from starvation exposure complex (proportion); **LS3d** = lamb survival to 3 d after birth (proportion); **LSWWT** = lamb survival to weaning (proportion).
3. **RSD** = residual standard deviation (using square root of linear variance).
4. **ns** = not significant (at P = 0.05).
5. Blank cells were not included in the final model as were either not significant or not applicable.

*P < 0.05; **P < 0.01.
models for LBW, LVB, LDD, LDSE, LS3d, and LSWWT included the fixed effects of flock, birth year of the lamb, litter size at birth, sex of lamb, and dam age and their interactions (Table 2). Flock × year effect was fitted to account for environment effects and is likely to have removed some breed effects as flock accounted for a breed type. Date of birth, lamb sex, and dam age effects as well as birth year of the lamb, litter size, flock, and their interactions with litter size and dam age were fitted regardless of significance. Table 2 reports the significance of the effects tested using the DMLitter model and subsequently retained for all models, if statistically significant at P < 0.05.

Table 3. Least squares means (±SE) for the effects of litter size at birth, dam age, and lamb sex on lamb survival and mortality traits recorded from birth to weaning using the DMLitter \(^1\) random effects model \(^2\)

| Lamb trait | LBW   | LVB   | LDD   | LDSE  | LS3d | LSWWT |
|------------|-------|-------|-------|-------|------|-------|
| No. of records | 103,537 | 75,408 | 73,660 | 73,694 | 97,424 | 97,424 |
| Litter size at birth |          |       |       |       |      |       |
| Singles     | 5.80 ± 0.0130 | 0.98 ± 0.0017 | 0.02 ± 0.0020 | 0.01 ± 0.0017 | 0.945 ± 0.0038 | 0.926 ± 0.0043 |
| Twins       | 4.81 ± 0.0112 | 0.98 ± 0.0013 | 0.02 ± 0.0015 | 0.02 ± 0.0012 | 0.898 ± 0.0027 | 0.870 ± 0.0031 |
| Triplets    | 4.10 ± 0.0135 | 0.95 ± 0.0017 | 0.04 ± 0.0018 | 0.04 ± 0.0015 | 0.810 ± 0.0038 | 0.752 ± 0.0042 |
| P-value     | ***   | ***   | ***   | ***   | ***  | ***   |
| Dam age, yr |       |       |       |       |      |       |
| 2           | 4.51 ± 0.0130 | 0.96 ± 0.0016 | 0.04 ± 0.0018 | 0.02 ± 0.0014 | 0.867 ± 0.0032 | 0.836 ± 0.0036 |
| 3           | 4.93 ± 0.0121 | 0.97 ± 0.0016 | 0.03 ± 0.0018 | 0.02 ± 0.0015 | 0.889 ± 0.0033 | 0.860 ± 0.0037 |
| 4           | 5.05 ± 0.0122 | 0.97 ± 0.0017 | 0.02 ± 0.0019 | 0.02 ± 0.0015 | 0.902 ± 0.0034 | 0.868 ± 0.0038 |
| 5           | 5.09 ± 0.0230 | 0.97 ± 0.0019 | 0.02 ± 0.0021 | 0.02 ± 0.0017 | 0.896 ± 0.0038 | 0.859 ± 0.0043 |
| 6+          | 4.99 ± 0.0143 | 0.97 ± 0.0021 | 0.03 ± 0.0023 | 0.03 ± 0.0019 | 0.876 ± 0.0040 | 0.833 ± 0.0046 |
| P-value     | ***   | ***   | ***   | ***   | ***  | ***   |
| Lamb sex    |       |       |       |       |      |       |
| Ram lamb    | 5.08 ± 0.0107 | 0.97 ± 0.0014 | 0.03 ± 0.0016 | 0.02 ± 0.0013 | 0.879 ± 0.0026 | 0.843 ± 0.0030 |
| Ewe lamb    | 4.76 ± 0.0107 | 0.98 ± 0.0014 | 0.02 ± 0.0015 | 0.02 ± 0.0012 | 0.893 ± 0.0026 | 0.860 ± 0.0029 |
| P-value     | ***   | ***   | ***   | ns\(^3\) | ***  | ***   |

\(^{1}\)DMLitter = random effects fitted include direct additive genetic effect + maternal genetic effect + temporary environmental effect of dam/year.

\(^{2}\)LBW = lamb birth weight (kg); LVB = lamb viability at birth (proportion); LDD = lamb death risk from dystocia (proportion); LDSE = lamb death risk from starvation exposure complex (proportion); LS3d = lamb survival to 3 d after birth (proportion); LSWWT = lamb survival to weaning (proportion).

\(^{3}\)ns = not significant (at P = 0.05).

\(**P < 0.001.

RESULTS

There was 8% lamb mortality up to 3 d of age and 2% of lambs born were not alive at birth (Table 2). Lamb mortality from birth to weaning age (approximately 100 d) was 12% (Table 2) and therefore two-thirds of lamb deaths occurred in the first 3 d from birth. The postmortem procedure identified 2% of all lambs born died from dystocia and 2% died from starvation exposure up to 3 d of age. The average LBW was 4.85 kg (Table 2).

The effects of litter size at birth, dam age, and lamb sex are reported in Table 3. Lamb birth weights were heaviest for single lambs, lambs born to older dams, and ram lambs (Table 3). Lamb survival rates were greater for single born lambs, lambs born to 4-yr-old dams, and ewe lambs (Table 3). Triplet born lambs were the lightest at birth and had decreased viability rates, greater death risk to dystocia and starvation exposure, and decreased survival rates to 3 d of age and to weaning age when compared with singles and twins. Lambs born to younger dams had lower birth weights, decreased viability rates, greater death risk to dystocia, and lower survival rates to 3 d and to weaning age. Lambs born to 6-yr-old dams and older dams had greater death risk to starvation exposure and similar low survival rates as 2-yr-old dams (Table 3). The relationship of environment and management effects on the lamb survival and death risk traits were explored in more detail by Everett-Hincks and Dodds (2008). Estimated variance components and genetic parameters for the lamb traits are shown in Tables 4 through 9 for the random effects models tested. For LBW, the heritability attributed to direct effects ranged from 0.13 to 0.14 while the heritability attributed to maternal effects (expressed when the ewe lamb produces progeny of her own) ranged from 0.18 to 0.32. For the traits diagnosed by postmortem procedure, that is, LVB, LDD, and LDSE, the direct heritabilities were less than 0.01 for all random effects models tested. The heritabi-
Table 4. Estimated variance components and genetic parameters (±SE) for lamb birth weight (kg) testing different random effects models

| Item                                | DMc       | DMcL      | DMDam     | DMLitter   |
|-------------------------------------|-----------|-----------|-----------|------------|
| No. of records                      | 103,537   | 103,537   | 103,537   | 103,537    |
| Trait mean ± RSD, kg                | 4.85 ± 0.607 | 4.85 ± 0.576 | 4.85 ± 0.603 | 4.85 ± 0.577 |
| $\sigma^2$ direct animal            | 0.088 ± 0.0063 | 0.082 ± 0.0061 | 0.087 ± 0.006 | 0.079 ± 0.006 |
| $\sigma^2$ maternal                 | 0.203 ± 0.0067 | 0.167 ± 0.0026 | 0.113 ± 0.006 | 0.159 ± 0.004 |
| $\sigma$ direct maternal covariance | −0.017 ± 0.0644 | −0.0092 ± 0.0061 | n/a        | n/a        |
| $\sigma^2$ permanent environment    | n/a       | n/a       | 0.065 ± 0.005 | n/a        |
| $\sigma^2$ litter                   | n/a       | n/a       | 0.062 ± 0.0027 | n/a        |
| $\sigma^2$ total genetic            | 0.274 ± 0.0057 | 0.231 ± 0.0072 | 0.239 ± 0.005 | 0.239 ± 0.005 |
| $\sigma^2$ total phenotypic         | 0.642 ± 0.0037 | 0.624 ± 0.0069 | 0.634 ± 0.004 | 0.634 ± 0.004 |
| Proportion of litter variation      | n/a       | 0.10 ± 0.004 | n/a       | 0.10 ± 0.004 |
| Proportion of dam variation         | n/a       | n/a       | 0.10 ± 0.007 | n/a        |
| $h^2$ direct                        | 0.137 ± 0.0095 | 0.132 ± 0.0101 | 0.138 ± 0.009 | 0.126 ± 0.009 |
| $h^2$ maternal                      | 0.316 ± 0.0100 | 0.267 ± 0.0124 | 0.179 ± 0.009 | 0.250 ± 0.005 |
| $h^2$ total                         | 0.426 ± 0.0073 | 0.370 ± 0.0084 | 0.317 ± 0.010 | 0.377 ± 0.007 |
| $r_{g}$ direct and maternal         | −0.127 ± 0.0450 | −0.078 ± 0.0084 | n/a        | n/a        |
| Log likelihood                      | −20,763.74 | −20,527.17 | −20,663.57 | −20,469.24 |

1The following random effects were tested and differed between models: DMc = direct additive genetic effect (D) + maternal genetic effect (M) + covariance between D and M; DMcL = D + M + covariance between D and M + temporary environmental effect of dam/year; DMDam = D + M + permanent environmental effect of dam; DMLitter = D + M + temporary environmental effect of dam/year.

2RSD = residual standard deviation (using square root of linear variance).

3n/a = not applicable.

4$r_{g}$ = genetic correlation.

Table 5. Estimated variance components and genetic parameters (±SE) for lamb viability at birth (proportion) testing different random effects models

| Item                                | DMc       | DMcL      | DMDam     | DMLitter   | LogitDMLitter |
|-------------------------------------|-----------|-----------|-----------|------------|---------------|
| No. of records                      | 75,408    | 75,408    | 75,408    | 75,408     | 74,739        |
| Trait mean ± RSD                    | 0.98 ± 0.145 | 0.98 ± 0.140 | 0.98 ± 0.144 | 0.98 ± 0.140 | 0.98 ± 0.140 |
| $\sigma^2$ direct animal            | 0.00008 ± 0.00005 | 0.00004 ± 0.00004 | 0.00005 ± 0.00004 | 0.000 ± 0.000 | 0.0000 ± 0.0000 |
| $\sigma^2$ maternal                 | 0.0011 ± 0.00001 | 0.0003 ± 0.00001 | 0.0002 ± 0.00001 | 0.0002 ± 0.0000 | 0.3539 ± 0.1116 |
| $\sigma$ direct maternal covariance | −0.0002 ± 0.00001 | −0.0001 ± 0.00007 | n/a        | n/a        | n/a           |
| $\sigma^2$ permanent environment    | n/a       | n/a       | 0.0011 ± 0.00001 | n/a        | n/a           |
| $\sigma^2$ litter                   | n/a       | 0.002 ± 0.0001 | n/a       | 0.002 ± 0.0001 | 0.5812 ± 0.1425 |
| $\sigma^2$ total genetic            | 0.001 ± 0.00001 | 0.0002 ± 0.00001 | 0.0002 ± 0.00001 | 0.0002 ± 0.0001 | 0.3539 ± 0.1117 |
| $\sigma^2$ total phenotypic         | 0.022 ± 0.00011 | 0.0219 ± 0.00013 | 0.022 ± 0.0001 | 0.022 ± 0.0001 | 4.225 ± 0.1021 |
| Proportion of litter variation      | n/a       | 0.09 ± 0.006 | n/a       | 0.09 ± 0.003 | 0.14 ± 0.032 |
| Proportion of dam variation         | n/a       | 0.05 ± 0.005 | n/a       | n/a        | n/a           |
| $h^2$ direct                        | 0.004 ± 0.0022 | 0.002 ± 0.0021 | 0.002 ± 0.0019 | 0.001 ± 0.0019 | 0.000 ± 0.000 |
| $h^2$ maternal                      | 0.049 ± 0.0056 | 0.014 ± 0.0044 | 0.008 ± 0.0033 | 0.009 ± 0.0028 | 0.084 ± 0.0263 |
| $h^2$ total                         | 0.045 ± 0.0037 | 0.008 ± 0.004 | 0.0102 ± 0.0035 | 0.01 ± 0.003 | 0.084 ± 0.0263 |
| $r_{g}$ direct and maternal         | −0.569 ± 0.2971 | −0.786 ± 0.5229 | n/a        | n/a        | n/a           |
| Log likelihood                      | 103,894.65 | 104,409.62 | 103,959.06 | 104,041.85 | −160,254.84  |

1The following random effects were tested and differed between models: DMc = direct additive genetic effect (D) + maternal genetic effect (M) + covariance between D and M; DMcL = D + M + covariance between D and M + temporary environmental effect of dam/year; DMDam = D + M + permanent environmental effect of dam; DMLitter = D + M + temporary environmental effect of dam/year; LogitDMLitter = logit transformation of DMLitter.

2RSD = residual standard deviation (using square root of linear variance).

3n/a = not applicable.

4$r_{g}$ = genetic correlation.
### Table 7. Estimated variance components and genetic parameters (±SE) for lamb death risk to starvation exposure (proportion) testing different random effects models

| Item                          | DMc   | DMcL  | DMDam | DMLitter | LogitDMLitter |
|-------------------------------|-------|-------|-------|----------|---------------|
| No. of records                | 73,694| 73,694| 73,694| 73,694   | 72,057        |
| Trait mean ± RSD              | 0.024 ± 0.146 | 0.024 ± 0.139 | 0.024 ± 0.144 | 0.02 ± 0.139 | 0.024 ± 0.139 |
| $\sigma^2$ direct animal      | 0.0002 ± 0.00006 | 0.00007 ± 0.00005 | 0.0001 ± 0.00004 | 0.000 ± 0.000 | 0.000000 ± 0.0000 |
| $\sigma^2$ maternal genetic   | 0.001 ± 0.0001 | 0.0002 ± 0.00009 | 0.0001 ± 0.0001 | 0.000 ± 0.000 | 0.1923 ± 0.1051 |
| $\sigma^2$ direct maternal covariance | -0.0002 ± 0.0001 | -0.0001 ± 0.00008 | n/a $^3$ | n/a | n/a |
| $\sigma^2$ permanent environment | n/a | n/a | 0.0015 ± 0.0001 | n/a | n/a |
| $\sigma^2$ litter             | n/a | 0.0027 ± 0.0001 | n/a | 0.003 ± 0.0001 | 0.7874 ± 0.1414 |
| $\sigma^2$ total genetic      | 0.0011 ± 0.0001 | 0.00005 ± 0.00008 | 0.0002 ± 0.0001 | 0.0002 ± 0.000 | 0.1923 ± 0.1049 |
| $\sigma^2$ total phenotypic   | 0.0224 ± 0.00012 | 0.0222 ± 0.00014 | 0.022 ± 0.0012 | 0.022 ± 0.0001 | 4.269 ± 0.1023 |
| Proportion of litter variation| n/a | 0.12 ± 0.006 | n/a | 0.12 ± 0.006 | 0.18 ± 0.03 |
| Proportion of dam variation   | n/a | n/a | 0.07 ± 0.005 | n/a | n/a |
| $h^2$ direct                  | 0.007 ± 0.0027 | 0.003 ± 0.0024 | 0.004 ± 0.0022 | 0.002 ± 0.0021 | 0.000 ± 0.000 |
| $h^2$ maternal                | 0.052 ± 0.2245 | 0.011 ± 0.0044 | 0.004 ± 0.0030 | 0.005 ± 0.0026 | 0.045 ± 0.0245 |
| $h^2$ total                   | 0.049 ± 0.0040 | 0.0021 ± 0.0038 | 0.007 ± 0.0035 | 0.007 ± 0.0031 | 0.045 ± 0.0245 |
| $r_g$ direct and maternal     | -0.517 ± 0.225 | -1.015 ± 0.4259 | n/a $^4$ | n/a | n/a |
| Log likelihood                | 100,725.6 | 101,381.94 | 101,244.43 | 101,380.24 | -15,107.3 |

1The following random effects were tested and differed between models: DMc = direct additive genetic effect (D) + maternal genetic effect (M) + covariance between D and M; DMcL = D + M + covariance between D and M + temporary environmental effect of dam/year; DMDam = D + M + permanent environmental effect of dam; DMLitter = D + M + temporary environmental effect of dam/year; LogitDMLitter = logit transformation of DMLitter.

2RSD = residual standard deviation (using square root of linear variance).

3n/a = not applicable.

4$r_g$ = genetic correlation.
### Table 8. Estimated variance components and genetic parameters (±SE) for lamb survival to 3 d of age (proportion) testing different random effects models

| Item                              | DMc        | DMcL       | DMDam      | DMLitter   | LogitDMLitter |
|-----------------------------------|------------|------------|------------|------------|---------------|
| No. of records                    | 97,424     | 97,424     | 97,424     | 97,424     | 96,533        |
| Trait mean ± RSD^2               | 0.92 ± 0.256 | 0.92 ± 0.244 | 0.92 ± 0.253 | 0.92 ± 0.244 | 0.92 ± 0.244 |
| σ^2 direct animal                | 0.0009 ± 0.0002 | 0.0007 ± 0.0002 | 0.0008 ± 0.0002 | 0.0001 ± 0.0002 | 0.0023 ± 0.0221 |
| σ^2 genetic maternal             | 0.0047 ± 0.0004 | 0.0013 ± 0.0003 | 0.0004 ± 0.0002 | 0.001 ± 0.0001 | 0.1886 ± 0.0363 |
| σ direct maternal covariance     | -0.0007 ± 0.0003 | -0.0004 ± 0.0002 | n/a        | n/a        | n/a           |
| σ^2 permanent environment        | n/a        | n/a        | 0.005 ± 0.0003 | n/a        | n/a           |
| σ^2 litter                       | n/a        | 0.0092 ± 0.0004 | n/a        | 0.009 ± 0.0004 | 0.5014 ± 0.0506 |
| σ^2 total genetic                | 0.0049 ± 0.00026 | 0.0011 ± 0.0003 | 0.001 ± 0.0002 | 0.002 ± 0.0002 | 0.212 ± 0.0391 |
| σ^2 total phenotypic             | 0.0705 ± 0.0003 | 0.0697 ± 0.0004 | 0.070 ± 0.0003 | 0.070 ± 0.0003 | 4.003 ± 0.0406 |
| Proportion of litter variation   | n/a        | 0.13 ± 0.005 | n/a        | 0.13 ± 0.005 | 0.13 ± 0.012 |
| Proportion of dam variation      | n/a        | n/a        | n/a        | n/a        | n/a           |
| h^2 direct                       | 0.013 ± 0.003 | 0.010 ± 0.003 | 0.011 ± 0.003 | 0.013 ± 0.003 | 0.006 ± 0.0055 |
| h^2 maternal                     | 0.066 ± 0.0055 | 0.018 ± 0.004 | 0.006 ± 0.003 | 0.013 ± 0.003 | 0.047 ± 0.0091 |
| h^2 total                        | 0.069 ± 0.0036 | 0.016 ± 0.004 | 0.017 ± 0.004 | 0.021 ± 0.003 | 0.053 ± 0.0097 |
| r_g^4 direct and maternal        | -0.332 ± 0.1401 | -0.437 ± 0.1971 | n/a        | n/a        | n/a           |
| Log likelihood                   | 78,301.28  | 78,913.89  | 78,652.25  | 78,912.58  | -172,517.79 |

1The following random effects were tested and differed between models: DMc = direct additive genetic effect (D) + maternal genetic effect (M) + covariance between D and M; DMcL = D + M + covariance between D and M + temporary environmental effect of dam/year; DMDam = D + M + permanent environmental effect of dam; DMLitter = D + M + temporary environmental effect of dam/year; LogitDMLitter = logit transformation of DMLitter.

2RSD = residual standard deviation (using square root of linear variance).

3n/a = not applicable.

4r_g = genetic correlation.

### Table 9. Estimated variance components and genetic parameters (±SE) for lamb survival to weaning age (proportion) testing different random effects models

| Item                              | DMc        | DMcL       | DMDam      | DMLitter   | LogitDMLitter |
|-----------------------------------|------------|------------|------------|------------|---------------|
| No. of records                    | 97,424     | 97,424     | 97,424     | 97,424     | 96,533        |
| Trait mean ± RSD^2               | 0.88 ± 0.296 | 0.88 ± 0.292 | 0.88 ± 0.293 | 0.88 ± 0.285 | 0.88 ± 0.285 |
| σ^2 direct animal                | 0.0007 ± 0.0002 | 0.0005 ± 0.0002 | 0.0006 ± 0.0002 | 0.0004 ± 0.0002 | 0.006 ± 0.015 |
| σ^2 genetic maternal             | 0.0053 ± 0.0005 | 0.0022 ± 0.0004 | 0.0008 ± 0.0003 | 0.0018 ± 0.0003 | 0.2275 ± 0.0299 |
| σ direct maternal covariance     | -0.0007 ± 0.0004 | -0.0003 ± 0.0003 | n/a        | n/a        | n/a           |
| σ^2 litter                       | n/a        | 0.0086 ± 0.0005 | n/a        | 0.009 ± 0.0006 | 0.2897 ± 0.0399 |
| σ^2 permanent environment        | n/a        | n/a        | 0.006 ± 0.0004 | n/a        | n/a           |
| σ^2 total genetic                | 0.0053 ± 0.0003 | 0.002 ± 0.0004 | 0.001 ± 0.0003 | 0.002 ± 0.0003 | 0.234 ± 0.0313 |
| σ^2 total phenotypic             | 0.0928 ± 0.0004 | 0.092 ± 0.0005 | 0.093 ± 0.0004 | 0.092 ± 0.0004 | 3.813 ± 0.03274 |
| Proportion of litter variation   | n/a        | 0.09 ± 0.005 | n/a        | 0.09 ± 0.005 | 0.08 ± 0.01 |
| Proportion of dam variation      | n/a        | n/a        | 0.06 ± 0.004 | n/a        | n/a           |
| h^2 direct                       | 0.007 ± 0.0023 | 0.006 ± 0.0022 | 0.006 ± 0.0021 | 0.005 ± 0.002 | 0.002 ± 0.0040 |
| h^2 maternal                     | 0.058 ± 0.0050 | 0.024 ± 0.0042 | 0.009 ± 0.0029 | 0.019 ± 0.003 | 0.059 ± 0.0078 |
| h^2 total                        | 0.058 ± 0.0033 | 0.022 ± 0.0039 | 0.015 ± 0.0033 | 0.025 ± 0.003 | 0.061 ± 0.0081 |
| r_g^4 direct and maternal        | -0.354 ± 0.1738 | -0.315 ± 0.2454 | n/a        | n/a        | n/a           |
| Log likelihood                   | 65,183.13  | 65,035.11  | 65,279.36  | 65,374.71  | -163,024.06 |

1The following random effects were tested and differed between models: DMc = direct additive genetic effect (D) + maternal genetic effect (M) + covariance between D and M; DMcL = D + M + covariance between D and M + temporary environmental effect of dam/year; DMDam = D + M + permanent environmental effect of dam; DMLitter = D + M + temporary environmental effect of dam/year; LogitDMLitter = logit transformation of DMLitter.

2RSD = residual standard deviation (using square root of linear variance).

3n/a = not applicable.

4r_g = genetic correlation.
ties attributed to maternal genetic effects ranged from 0.01 to 0.08 for LBW, LDD, and LDSE (Tables 5, 6, and 7).

The direct heritabilities for LS3d and LSWWT were 0.01, whereas the herdabilities attributed to maternal genetic effects ranged from 0.01 to 0.07 depending on the random effects model tested for both traits (Table 8 and 9). Log likelihood values can be used to compare the random effects models: DMc, DMcL, DMDam, and DMLitter. The DMLitter model was the best fit for LSWWT and both the DMcL and DMLitter models were of similar and best fit for LBW, LDD, LDSE, and LS3d according to their log likelihood values (Tables 5 through 9).

Log likelihoods cannot be used to compare the linear and logistic models; therefore, prediction error variances were calculated, as described in the methodology, to assess whether LogitDMLitter was a better fit for the binary traits recorded between birth and 3 d of age and survival to weaning age.

LogitDMLitter model was a slightly better fit than the nontransformed DMLitter random effects model (Table 10). To our knowledge, this is the first known genetic analysis of lamb birth weight (LBW; kg) with lamb traits recorded between birth and 3 d of age and survival to weaning age that Logit + Litter (LogitDMLitter) models1

| Trait | DMLitter model | LogitDMLitter | Correlation |
|-------|----------------|---------------|-------------|
| LBW   | 0.02193698     | 0.02198027    | 0.9069764   |
| LDD   | 0.02232457     | 0.02238533    | 0.8845866   |
| LDSE  | 0.07104967     | 0.0712064     | 0.921628    |
| LS3d  | 0.06880103     | 0.06879517    | 0.9505252   |
| LSWWT | 0.12576084     | 0.12606023    | 0.9833252   |

1DMLitter = direct additive genetic effect + maternal genetic effect + temporary environmental effect of dam/year; LogitDMLitter = logit transformation of DMLitter.

2LBW = lamb viability at birth (proportion); LDD = lamb death risk from dystocia (proportion); LDSE = lamb death risk from starvation exposure complex (proportion); LS3d = lamb survival to 3 d after birth (proportion); LSWWT = lamb survival to weaning (proportion).


dystocia rates (positive and moderate). The maternal to maternal genetic correlations are expressed a generation later when the ewe lambs are bred. The maternal genetic correlations of LBW with LS3d and LSWWT were low and positive, whereas the maternal genetic correlations of LBW with LVB and LDSE were low and negative. The maternal genetic correlation between LBW and LDD was moderate and positive; therefore, the genes responsible for a dam to have heavier lambs at birth are potentially some of the same genes responsible for higher progeny dystocia rates (Table 11).

**DISCUSSION**

To our knowledge, this is the first known genetic analysis of lamb survival and mortality risk factors where the random effects models have been explored in some depth. Total (direct + maternal) heritability estimates were low (0.01 to 0.08) for the survival and mortality traits and moderate (0.32 to 0.43) for LBW. Heritability estimates have been previously derived for cause of lamb mortality by Southey et al. (2002). Southey et al. (2002) grouped dystocia and starvation-related deaths into 1 category and reported a direct heritability of 0.11 and a maternal heritability of 0.18. Direct heritabilities for LDD and LDSE in our study were <0.01 whereas the maternal heritabilities were 0.01. For the traits studied, the maternal heritabilities accounted for at least half to two-thirds of the total genetic variation. This is promising; however, genetic variation attributed to maternal effects is expressed a generation later when the ewe lamb produces progeny of her own. Petersson and Danell (1985) suggest that the maternal genetic influence of lamb survival, that is, the dam’s provision of an environment in which the offspring performs, is more important than the directly transmitted genetic component of the offspring. This was observed for all of the traits in this study.

| Trait | \( r_{gp} \) | \( r_{gd} \) | \( r_{gm} \) |
|-------|-------------|-------------|-------------|
| LBW   | 0.03 ± 0.004 | −0.61 ± 0.417 | −0.16 ± 0.069 |
| LDD   | −0.04 ± 0.004 | 0.45 ± 0.309 | 0.20 ± 0.098 |
| LDSE  | −0.10 ± 0.004 | Nonestimable | −0.15 ± 0.066 |
| LS3d  | 0.15 ± 0.003 | −0.27 ± 0.110 | 0.14 ± 0.054 |
| LSWWT | 0.17 ± 0.003 | −0.28 ± 0.141 | 0.09 ± 0.043 |

1LBW = lamb viability at birth (proportion); LDD = lamb death risk from dystocia (proportion); LDSE = lamb death risk from starvation exposure complex (proportion); LS3d = lamb survival to 3 d after birth (proportion); LSWWT = lamb survival to weaning (proportion).

\( r_{gp} \) = phenotypic correlation; \( r_{gd} \) = direct to direct genetic correlation; \( r_{gm} \) = maternal to maternal genetic correlation.
Overall mortality reported by Southey et al. (2002) was 15.2% from birth to 4 wk whereas the mortality rate from birth to weaning (100 d) in the current study was 12%. The total heritability for survival reported by Southey et al. (2002) was 0.22 using a maternal genetic model and 0.15 using a sire model and did not investigate the random environmental effect of dam. Estimates of total heritability for preweaning lamb survival in the current study were similar to those reported by Morris et al. (2000; 0.029) and Brien et al. (2010; 0.01). However, they were lower than that reported by Lopez-Villalobos and Garrick (1999; 0.042), Everett-Hincks et al. (2005; 0.16, using a different dataset and model) and Cloete et al. (2002; 0.28). Reported estimates of the genetic components of lamb survival indicate limited genetic variation (Petersson and Danell, 1985; Hall et al., 1995; Lopez-Villalobos and Garrick, 1999; Morris et al., 2000; Fadilli and Leroy, 2001; Cloete et al., 2002; Everett-Hincks et al., 2005; Safari et al., 2005) and that lamb survival is controlled mainly by nonadditive genetic factors.

This study undertook analyses to investigate maternal effects, both genetic and environmental, by fitting appropriate random effects for each animal in the data. Analyses were performed to investigate the magnitude of the heritabilities when the random environmental effect of dam and litter (dam within year) were fitted. The permanent environmental of dam accounted for 5 to 10% of the total variation whereas the environment of litter (dam within year) accounted for 8 to 18%, depending on the model fitted. Total heritabilities were about 50% lower for the traits studied when accounting for the random environmental effect of litter compared to not accounting for the environment effect of the dam. The expression of maternal effects is sex limited, occurs at breeding age of the female, and lags by 1 generation and therefore data structure is important to allow good estimates of the component effects. According to Clement et al. (2001), the data structure may have led to biased variance estimates. Clement et al. (2001) also report from simulations that the lack of genetic connectedness between years suggests that the maternal environmental effects can be overestimated. The genetic pathways of maternal genetic and environmental effects were investigated further using the sampling correlations of parameters (variance components) within a trait model in an attempt to better understand whether the correct model was fitted for analysis (Meyer, 1992).

For the LS3d trait, the sampling correlations between the estimate of maternal genetic effect and the estimate of environmental effect of litter were moderate to strongly negative for the models investigated (DMLitter, −0.42, and LogitDMLitter, −0.56) and similar for the estimated maternal genetic effect and estimated environmental effect of dam (DMDam, −0.60). These indicate that the data structure may not have allowed clean and therefore unbiased estimates of the component effects and therefore the total heritabilities may be overestimated when not accounting for the maternal environment of either dam or litter. It appears that the DMLitter model better apportions the random effect of environment from the maternal genetic effect than that for the DMDam model for the LS3d trait and requires further investigation using a simulated model method to determine why this could be happening. New Zealand’s genetic evaluation service, SIL, does not currently adjust lamb survival for maternal environment effects and therefore it is likely that the maternal genetic component has absorbed some of the random environmental variance of the dam (litter effect and a maternal permanent environmental effect). Breeding values derived for traits accounting for the maternal environment are more conservative and should be considered when designing animal improvement programs for lamb survival and mortality traits. Meyer (1992) recommended that further research was required to evaluate the implications of large sampling variances and covariances on the accuracy of selection indexes including both direct and maternal effects, that is, the expected loss in selection response, because inaccurately estimated parameters have been used to derive index weights.

The total heritability for LBW was moderate in this study (0.38) and similar to heritabilities summarized by Safari et al. (2005). The direct genetic effect was low in our study with most genetic variation in LBW attributed to maternal genetic effects (0.13 vs. 0.25). Estimates reviewed by Safari et al. (2005) for dual purpose breeds range from 0.04 to 0.24 for direct genetic effects and 0.07 to 0.30 for maternal genetic effects. The majority of breeders in New Zealand have not been recording LBW and therefore have been unable to select for it directly. They have been selecting on weaning weight and growth rate and have therefore been selecting indirectly for greater LBW. Moderate positive genetic correlations between birth weight and growth rate and between birth weight and weaning weight have been reported in the review by Safari et al. (2005). Therefore, it is likely that the genes involved in heavier lambs at birth are similar to those involved in faster growing lambs and larger lambs weaned. However, this selection method could lead to heavier mature weights, which are undesirable for some farming systems, and therefore there could be potential for holding LBW constant and genetically improving lamb growth rates or vice versa depending on the environment, feed availability, and overall farm system.

Lamb birth weight is better fitted as a quadratic effect than a linear effect on LVB, LDD, LDSE, LS3d, and LSWWT, as an optimum birth weight was shown to be important; that is, low and high birth weights are not favorable for these traits (Everett-Hincks and Dodds, 2008). Correlations assume a linear relationship. The
genetic correlation estimates of LBW with the lamb survival and mortality traits in this study have a wide range and have relatively large standard errors and therefore should be interpreted with caution. The sign was unfavorable for survival traits with moderate genetic correlations with LBW and suggests that genetic selection for greater LBW will decrease LVB and survival to 3 d of age and to weaning age in the population studied.

The animals used in this study were of various breeds and breed mixes. Additional analyses were undertaken where breed percentages of the main breeds were specifically fitted and results were similar to the case found for a set of production and disease traits in New Zealand sheep (Pickering et al., 2012). Separate, subset analyses have been performed for each of Romney, Perendale, Coopworth, Texel, crossbreds (2 breed combinations), and composites (combinations of more than 2 breeds). The total genetic variance (direct genetic + maternal genetic) estimated for these subsets, using the DMLitter model for the survival to 3 d trait, did not differ by more than 2 standard errors from the corresponding value from the full data set. For the LBW trait, the total genetic variance did not differ by more than 2 standard errors for the Romney, Coopworth, Texel, and composite subsets and did differ by up to 3 standard errors for the Perendale and crossbreds. Perendales and crossbreds make up less than 20% of the flocks studied and that there is little birth weight information from these groups recorded in industry, so the models and estimates presented here still provide a practical and useful way forward for the industry. This may need to be revisited as more information, especially birth weight, becomes available and as industry breeds change.

The view of Southey et al. (2002) is that ignoring the lamb mortality traits involved in survival data may hide important genetic differences. However, our larger study has shown that the component lamb mortality traits are not worthy of inclusion in animal breeding programs as the survival traits to weaning and LS3d have higher heritabilities. Effective animal breeding programs can be formulated based on accurate recording of survival to weaning. This phenotype is easier to record, requiring less labor at lambing time, and therefore is favorable given its slightly higher genetic variance than for the death risk traits studied.

This study has also shown that the total heritabilities may be overestimated when not accounting for maternal genetic and environment effects and in particular accounting for the random environmental effect of litter (dam/year).

**Implications**

Heritability estimates for the lamb survival and mortality traits in the current study are very low; however, genetic progress could be made by selecting and culling ewe lambs based on their estimated breeding values for the lamb mortality and survival traits as maternal heritabilities proved higher. There is little to no benefit in recording postmortem traits above accurate recording for lamb survival to weaning for the population studied.

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