

The genetic and phenotypic associations between lamb survival outcomes and other traits recorded at lambing

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ABSTRACT

Context. Australian sheep breeding values (ASBVs) for lambing ease (LE) are estimated by Sheep Genetics, by using a threshold animal model at the lamb level, in a tri-variate analysis that includes data on birth weight, gestation length and lambing ease score. The implications of these traits for lamb survival, or the use of other indirect traits to improve accuracy of ASBVs for LE, are not currently being considered. Ultimately, it is desirable to extend the analysis to outcomes for individual lamb survival. **Aim.** The present study investigated implications of LE for lamb survival outcomes, accounting for litter size, and examined associations with other traits recorded at or shortly after lambing in maternal sheep breeds. **Methods.** Equivalent linear models were used to compare lamb- and ewe-level models with various combinations of additional random effects. In particular, lambing ease was treated as a different trait for single-born and twin-born lambs, to identify changes in genetic correlations associated with litter size between LE and other traits. Other traits included lambs recorded dead at birth, survival to weaning, lamb birth weight, gestation length and maternal behaviour score. **Key results.** Individual lamb survival outcomes inferred from field data and dead at birth lambs, are lowly heritable traits influenced by both direct and maternal effects. Lamb survival is positively correlated with birth weight, but negatively correlated with gestation length, lambing ease score (increasing lambing difficulty) and dead at birth lambs. Genetic and phenotypic correlations demonstrated that birth weight and lambing ease are antagonistic traits, more so for single-born lambs. Genetic correlations were moderate between dead at birth lambs and LE (0.40–0.45 singles; 0.15–0.36 including data from twins) or lamb survival (–0.63 to –0.81 singles; –0.00 to –0.23 including data from twins) and can add to the accuracy of genetic evaluation for these traits. In contrast, maternal behaviour score was predominantly an ewe trait, and will therefore add to accuracy of evaluation only for maternal effects. Lamb-level models appeared to underestimate heritability, sometimes compensated for by larger variance, and over-estimate genetic correlations for some traits relative to ewe-level models. **Conclusions.** Expanding the current lambing ease analysis to include dead at birth records and lamb survival outcomes would provide more detailed options for breeders to develop breeding goals to improve outcomes for both ewes and lambs. Further work is required to expand analyses to include threshold and continuous traits and understand genetic contributions to ewe survival traits. **Implications.** Relative selection emphasis on LE and birth weight must be considered in light of the expected litter size in which lambs will be born, to ensure favourable outcomes for lamb survival overall. Accuracy of genetic evaluation for LE can be improved using data on dead at birth. Equivalent ewe model analyses are possible. Completeness of pedigree, availability of informative lamb level data and integration with other traits are also factors to consider for the choice between operational lamb- versus ewe-level models for genetic evaluation systems.

Keywords: birth weight, correlation, gestation length, heritability, lambing difficulty, lambing ease, linear model, maternal behaviour score, maternal effects.

Introduction

The highest risk period for ewe (Mavrogianni and Brozos 2008) or sow (Sasaki and Koketsu 2008) mortality is around the time of parturition, in the periparturient period, or following dystocia and during lactation under grazing conditions for beef cattle. Similarly, the majority of lamb (Refshauge *et al.* 2016), calf (Patterson *et al.* 1987; Bunter *et al.* 2014) and piglet (Marchant *et al.* 2000) deaths occur within the first few days after parturition. In these species, dam and offspring vitality and survival at these times are the outcome of complex processes, including factors affecting both individuals before, during and after the parturition process. However, individual lamb and ewe survival post-lambing is rarely reliably recorded in field data. Therefore, it can be difficult to identify data-based strategies to improve survival outcomes for both ewes and their progeny.

Breeders and producers affected by an unacceptable incidence of problems at lambing, such as many ewes requiring assistance, lambs dead at birth and/or excessive ewe or lamb deaths post-lambing, can record additional data at this time. Lambing ease (LE) score and lamb birth weight (BWT) are two traits recorded to avoid deaths at lambing resulting from difficult births. However, many lambing events are not observed directly even with twice daily lambing rounds and therefore many flocks have ewes with an 'unobserved' lambing ease. Live lambs showing evidence of a difficult but unobserved lambing can be assigned a score representing a low degree of lambing difficulty, providing lambing rounds are regular and unassisted contemporaries are also recorded as unassisted, rather than unobserved (Sheep-Genetics 2022). Sheep Genetics provides breeding values specifically for LE, which are derived from a lamb level analysis that includes only gestation length, individual lamb BWTs and LE scores (Brown 2007; Li and Brown 2016). In this scenario, LE is essentially an indirect trait that is used to infer typically unrecorded lamb and ewe survival. However, other traits that could potentially contribute to understanding lamb survival outcomes include the lamb survival outcome itself (dead or alive), inferred from the data, along with 'dead at birth' (DAB) lambs and maternal behaviour score, recorded by breeders. Therefore, for the most accurate breeding values for lamb survival, a potential alternative is to include all the above-mentioned traits affecting lamb survival in a combined lamb level analysis. However, the suitability and ability to do this is contingent on the recording characteristics and expression for each trait, the availability of pedigree and genotypes for both lambs and their dams, and the ability to model each trait appropriately.

In the current genetic evaluation system for Sheep Genetics, lamb survival outcomes are analysed as the ewe rearing ability (ERA), after accounting for birth type (Bunter *et al.* 2018, 2019, 2021). ERA is defined as the proportion of lambs born that survive and can be evaluated even where

parentage of lambs is unknown. ERA tends to have higher heritability than does lamb survival. Traits included in the analysis of ERA include maternal behaviour score (MBS) noted above. However, an alternative approach suggested for improving lamb survival (Brien *et al.* 2010) is genetic evaluation from a lamb level analysis. This analysis is more complex, because both direct and maternal genetic influences must be accommodated, implying that full pedigree is available on both lambs and their dams. This is an uncommon scenario in many extensively managed flocks, especially for dead lambs. Further, the lamb survival trait is binary, observed only once, dead lambs are not selection candidates, and parents do not provide useful multi-generational phenotypes for increasing accuracy, as all recorded parents have the same phenotype (i.e. they are survivors). The utility of a lamb level analysis for lamb survival outcomes requires further investigation from industry-supplied data, in the absence of other traits that could be observed for individual lambs (e.g. interval to suckle, cold tolerance; Brien *et al.* 2010; Dwyer *et al.* 2016)) that might be considered useful traits to improve accuracy for lamb survival in a lamb level analysis.

The purpose of this study was to investigate heritabilities for lamb survival in maternal breeds, establish the importance of litter size for associations among traits, and evaluate the number of traits that could potentially be considered in future LE analysis.

Materials and methods

Data

Lamb survival data from the Sheep Genetics (SG) LAMBPLAN maternal breed database were extracted for flocks recording LE scores, along with any accompanying data for lamb BWTs (kg) and DAB lambs. In this study, LE score refers to the 5-score system (1–5) from the scoring guide provided by Sheep-Genetics (2022), whereby scores are from Score 1 = 'unassisted' to Score 3 = 'hard pull', and Scores 4 and 5 represent 'malpresentation' and 'veterinary assistance'. Therefore, an increasing score represents an increasing difficulty of lambing. Preliminary characterisation of the data identified that LE presented by breeders could be incomplete for all lambs within a litter. Therefore, lambs with missing LE scores within a litter with siblings recorded for LE were assigned values of 1 = unassisted, to ensure unrecorded full-sibs had scores. Lamb survival traits included lambs identified by breeders as DAB (0 = alive, 1 = dead), or inferred through survival to weaning (WEAN: 0 = dead, 1 = alive), or survival of lambs alive at birth to weaning (LWEAN: 0 = dead, 1 = alive, for DAB ≠ 1). Lambs not alive at birth (DAB) or weaning (lamb not reared, RT = 0) were identified directly by breeders and also confirmed through further data interrogation, by the complete absence of data for lambs recorded after birth in

the Sheep Genetics database. Full-sib lambs had a common birth type (BT, 1-N), MBS (from 1 = good to 5 = poor) and the same gestation length (GL, days), when present. Only lambs resulting from artificial insemination (AI) can have GL known. Flock-years with <80% of dams known were excluded from the data for analyses, along with litters containing more than four lambs recorded at birth, or where the number of lambs identified did not match their litter birth-type details. The resulting pedigree included 1.5 million animals, 13 836 sires, and 352 417 dams extended over 14 generations, with data from up to 733 811 litters (lambing events).

Systematic effects

Models for all traits included the systematic effects of contemporary group (CG), defined as site-year of lambing concatenated with dam-sire breed identifiers, along with litter size and age of dam groupings. Least-squares means (LSM) for BWT, DAB, and WEAN by litter-size group (four levels: 1, 2, 3, 4), age-of-dam group (six levels: 1, 2, 3-5, 6-8, 8+, unknown) and LE score (six levels: scores 1-5, unknown) were estimated using SAS (SAS Software; https://www.sas.com/en_au/home.html), fitting CG and each effect without interaction terms, for illustration. The LSM for LE by litter-size group or dam-age group were obtained concurrently.

Parameter estimates for individual traits

To obtain parameter estimates, the following two primary scenarios were considered:

1. Traits were considered as traits of the lamb, fitting an animal model with direct additive genetic effects of the lamb (a) along with maternal genetic (m) and non-genetic effects treated as additional random effects. Maternal non-genetic effects included permanent environmental effects of the dam (dpe), to accommodate repeated records per dam both within (i.e. full-sibs) and across (i.e. annual lambing) years. Models including the common litter effect (c), fitted to full-sibs within a litter, and dpe concurrently were also investigated. These models will be referred to as lamb-animal models.
2. Traits were represented as traits of the ewe, where lamb phenotypes were averaged within birth litter to generate a single trait value, subsequently analysed as a trait of the ewe. These models fitted ewe as the genetic effect at the animal level (m), non-genetic effects of the ewe to accommodate repeated records (pe), and included or excluded service sire effects (i.e. sire of the lamb, ss), to provide an alternative way to estimate the additive genetic variance for additive direct genetic effects of the lamb's genotype. Relationships between ss effects were accommodated through the complete numerator relationship matrix (NRM), common to both scenarios. The estimate of heritability of direct genetic effects for lambs was

assumed to be $4 \times$ sire variance/phenotypic variance. These models will be referred to as ewe-sire models.

Birth type of the lamb(s) is equivalent to litter size of the ewe, and is not influenced by each individual lamb's genes (i.e. a ewe trait only). Similarly, GL and MBS do not differ among full-sib lambs, but initiation of parturition affecting GL is known to be influenced by both fetal signals and maternal hormones (Liggins *et al.* 1973), and can therefore be considered as a trait of both the lamb(s) and dam. Conversely, MBS is expressed through scoring ewe behaviour, and should be treated as a trait of the ewe. All other traits (LE, BWT, LWEAN, WEAN) had the possibility for within-litter variability through different values for individual lambs.

For traits where the alternative models could be biologically meaningful, equivalence, or otherwise of these alternative models was demonstrated through comparing estimates from single-born litters only. In addition, the influence of birth type on parameter estimates in both scenarios was illustrated through adding or subtracting litter-size group from the models for estimation. The pedigree was constant across both scenarios, noting the one generation difference between lamb-animal and ewe-sire level models.

All traits were analysed in univariate models to estimate genetic parameters, fitting contemporary group and age-of-dam or ewe-age group as systematic class effects, as described above.

Correlations among traits

Correlations among all trait pairs were first estimated for single-born litters, where the explicit estimation of common litter effects is not required, but the number of records per ewe was significantly reduced. In subsequent analyses, the phenotype for lambing ease was used to construct different traits for single (LE1) and twin litters (LE2) only, and these traits were used in tri-variate analyses with each of the other traits to re-estimate genetic correlations separately for litters containing either single or twin births. Since ewes typically have both single and multiple births across their lifetime, maternal genetic and dam permanent environmental effects were fitted to be common across LE1 and LE2. All analyses for parameter estimation were performed using ASREML (Gilmour *et al.* 2015).

Results

Data characteristics

GL and MBS had relatively few records in comparison to other traits (Table 1). The percentage of lambs with augmented LE records was 8.9% of all lambs born in litters, with a least one lamb scoring an LE of ≥ 1 . Only a small percentage of all maternal breed flocks and animals are recorded for LE and/or DAB, with few lambs recorded for lambing ease with an LE of

Table 1. Data characteristics for each trait when analysed as either a lamb or ewe trait.

Trait	Lamb traits			Ewe traits		
	N	Mean (s.d.)	Min-max	N	Mean (s.d.)	Min-max
GL	34 159	147 (2.50)	131–161	20 513	147 (2.57)	131–161
MBS	n.a.	n.a.	n.a.	41 854	2.03 (0.96)	1–5
BWT	441 982	4.88 (1.04)	0.50–10.0	266 446	5.00 (1.02)	0.50–10.0
LE	317 174	1.01 (0.14)	1–3	175 937	1.02 (0.16)	1–3
DAB	395 213	0.074 (0.26)	0/1	230 946	0.070 (0.23)	0–1.0
LWEAN	1 217 543	0.837 (0.37)	0/1	702 446	0.841 (0.30)	0.25–1.0
WEAN	1 234 956	0.817 (0.39)	0/1	698 730	0.850 (0.30)	0–1.0

Ewe traits are calculated as the average of their lamb records, per litter.

GL, gestation length (days); MBS, maternal behaviour score (1–5); BWT, birth weight (kg); LE, lambing ease score (1–3); DAB, dead at birth (0 = alive, 1 = dead); WEAN, lamb weaned (0 = not weaned, 1 = weaned); LWEAN, live lamb at birth weaned (0 = not weaned, 1 = weaned).

>1 (1.2%). In contrast, more lambs were recorded for DAB and were reported as DAB = 1 (7.4%). The maternal breeds included within this analysis were characterised by a high mean litter size (1.75 lambs per lambing) for Australian sheep, consistent with maternal breeds. BWT averages differed depending on whether they were calculated from records for individual lambs (4.88 kg) or averages for ewes (5.00 kg), demonstrating bias in means associated with multiple lambs per litter.

Systematic effects

Least-squares means for the effects of birth-type group, age of dam group and LE score for BWT, DAB, WEAN and LE on the basis of individual-lamb data are shown in Table 2.

Litter size and age of dam

Larger litters (increasing birth type) had a higher incidence of DAB, lower individual lamb BWT and reduced survival of lambs until weaning, as expected. However, trends with litter size varied. Up to a litter size of three, the relationship between

litter size and lamb BWT was effectively linear. In contrast, the impact of LS for DAB and WEAN was most evident and increased as LS exceeded 2. Therefore, the association between LS and lamb survival was strongly non-linear. Maiden ewes had a higher DAB, despite a lower BWT, along with more LE scores of >1 and a lower WEAN. Relative to other ewe age groups, 3 to 5-year-old ewes had the highest WEAN. Lambing difficulties occurred more frequently in larger litters and for very young dams.

Lambing ease

As lambing difficulty increased from Scores 1 to 3, BWT and DAB increased and WEAN reduced. Thus, higher BWT was associated with higher LE scores (more difficult births) but, conversely, also higher lamb survival. Increased DAB was also associated with increased losses of live-born litter mates until weaning (not shown), providing separate evidence for a common litter effect on lamb survival. The trends for increasing LE with DAB, WEAN or LWEAN were also non-linear.

All associations were significant (Table 2, all $P < 0.0001$) and non-linear over the full range of possible levels,

Table 2. Least-squares means for the effect of birth litter size, age of dam group and lambing ease score on individual birth weight (BWT), dead at birth (DAB, $\times 100$), lambs weaned (WEAN, $\times 100$) and lambing ease score (LE). LSM with different letters within trait differ significantly ($P < 0.05$).

Level	Factor										
	Birth-type group				Age of dam group				Lambing ease score		
	BWT	DAB	WEAN	LE	BWT	DAB	WEAN	LE	BWT	DAB	WEAN
1	5.29a	2.2a	89.0a	0.99a	3.62a	4.4a	74.2a	1.01a	4.93a	2.1a	85.3a
2	4.58b	2.5a	84.5b	0.99a	4.22b	3.0b	83.3b	1.00b	5.50b	24.7b	58.4b
3	3.93c	5.5b	71.5c	1.01b	4.62c	2.4c	86.4c	0.99c	5.84c	36.3c	47.1c
4	3.65d	9.4c	63.6d	1.02b	4.69d	3.1b	83.2b	1.00b	5.18d	37.2c	44.6c
5	n.a.	n.a.	n.a.	n.a.	4.66d	3.4abc	79.7d	0.92d	5.03ad	18.7d	44.3c
Unknown	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	4.82e	3.3e	82.7d

Ewe traits are calculated as the average of their lamb records, per litter.

BWT, birth weight (kg); DAB, dead at birth (0 = alive, 1 = dead); WEAN, lamb weaned (0 = not weaned, 1 = weaned); LE, lambing ease score (1–5), including malpresentations and veterinary assistance for illustration.

suggesting that correlations will be influenced by population production levels (i.e. litter size) and other important systematic factors. Further, extreme levels for LE (e.g. Score 3) were poorly represented in the data. Importantly, the trends observed for BWT with LE, DAB with LE and WEAN with LE were not sustained for LE scores of >3, supporting the use of 1–3 scores only for analyses of LE, as typically used in models to evaluate lambing ease. Animals unrecorded for LE were lighter, with slightly elevated DAB and lower WEAN than for LE = 1 (unassisted) animals. This suggests the augmentation of missing LE records to LE = 1 for unobserved full-sibs in litters with LE scores should be an appropriate strategy to avoid partially recorded litters.

Model comparisons from univariate analyses

Parameter estimates from univariate analyses, treated as lamb or ewe traits, using the complete data, are shown in Table 3. Additive direct and maternal genetic contributions to BWT and GL were moderate to high. MBS was a moderately heritable trait of the ewe. Heritability estimates and additive maternal effects for all other traits (DAB, LE, LWEAN, WEAN) were very low, but with evidence for genetic contributions from sires to outcomes for lambs for these traits in ewe–sire models. Model comparisons suggest that the estimates of heritabilities for all traits may potentially be biased downward in lamb–animal models relative to comparable estimates obtained from ewe–sire models, but variances were higher

Table 3. Estimates of heritability (h^2_{lamb} , h^2_{ewe}), common litter effects (c^2), permanent environmental effects (ped^2 , pe^2) of the dam or ewe, maternal genetic (m^2) and service sire effects (ss^2), along with the residual (VE) and phenotypic variance (VP), from univariate analyses using the complete data, when analysed as either a lamb (lamb–animal models) or ewe (ewe–sire models) trait.

Trait	Lamb–animal models							Ewe–sire models					
	Model*	h^2_{lamb}	c^2	ped^2	m^2	VE	VP	h^2_{ewe}	pe^2	ss^2	VE	VP	* h^2_{lamb}
GL	–LS	–	–	–	–	–	–	0.21	0.00	–	2.66	3.39	n.a.
	+LS	–	–	–	–	–	–	0.22	0.00	–	2.64	3.36	n.a.
	+sire	–	–	–	–	–	–	0.21	0.01	0.13	2.35	3.58	0.51
MBS	–LS	–	–	–	–	–	–	0.14	0.13	–	0.498	0.681	n.a.
	+LS	–	–	–	–	–	–	0.14	0.13	–	0.496	0.678	n.a.
	+sire	–	–	–	–	–	–	0.14	0.13	0.01	0.493	0.679	0.02
BWT	–LS	0.14	0.38	0.05	0.12	0.260	0.854	0.18	0.05	–	0.589	0.766	n.a.
	+LS	0.17	–	0.12	0.15	0.389	0.688	0.21	0.05	–	0.458	0.619	n.a.
	+LS	0.15	0.28	0.05	0.14	0.265	0.682	–	–	–	–	–	n.a.
	+sire	–	–	–	–	–	–	0.20	0.05	0.05	0.439	0.631	0.21
LE	–LS	0.01	0.62	0.17	0.02	0.0045	0.025	0.02	0.19	na	0.020	0.026	n.a.
	+LS	0.03	–	0.53	0.02	0.011	0.027	0.02	0.19	na	0.020	0.025	n.a.
	+LS	0.01	0.63	0.17	0.02	0.0045	0.025	–	–	–	–	–	n.a.
	+sire	–	–	–	–	–	–	0.02	0.19	0.00	0.020	0.025	0.01
DAB	–LS	0.05	0.25	0.01	0.05	0.045	0.065	0.02	0.01	–	0.047	0.048	n.a.
	+LS	0.05	–	0.10	0.01	0.054	0.065	0.02	0.01	na	0.047	0.048	n.a.
	+LS	0.03	0.25	0.01	0.01	0.045	0.064	–	–	–	–	–	n.a.
	+sire	–	–	–	–	–	–	0.02	0.01	0.02	0.046	0.048	0.09
LWEAN	–LS	0.04	0.12	0.02	0.01	0.114	0.139	0.02	0.03	na	0.084	0.088	n.a.
	+LS	0.04	–	0.04	0.01	0.113	0.123	0.02	0.03	–	0.084	0.088	n.a.
	+LS	0.04	0.09	0.01	0.01	0.106	0.123	–	–	–	–	–	n.a.
	+sire	–	–	–	–	–	–	0.02	0.03	0.02	0.081	0.087	0.10
WEAN	–LS	0.04	0.12	0.02	0.01	0.114	0.139	0.02	0.02	na	0.074	0.078	n.a.
	+LS	0.04	–	0.04	0.01	0.124	0.136	0.02	0.02	na	0.073	0.076	n.a.
	+LS	0.04	0.10	0.01	0.01	0.115	0.136	–	–	–	–	–	n.a.
	+sire	–	–	–	–	–	–	0.02	0.02	0.02	0.072	0.077	0.09

All s.e. between 0.001 and 0.01, except GL with s.e. = 0.02. Ewe traits are calculated as the average of their lamb records, per litter. Model*, litter size excluded (–LS) or included (+LS) in the model; +sire, sire of lamb added as a random effect in the +LS model. * h^2_{lamb} , heritability calculated from estimate of service sire variance. GL, gestation length (days); MBS, maternal behaviour score (1–5); BWT, birth weight (kg); LE, lambing ease score (1–3); DAB, dead at birth (0 = alive, 1 = dead); WEAN, lamb weaned (0 = not weaned, 1 = weaned); LWEAN, live lamb at birth weaned (0 = not weaned, 1 = weaned).

for some traits in lamb–animal models. For comparison, under an ewe–sire + LS model, the contribution of sire genes to lamb BWT heritability was $0.053 \times 4 = 0.21$ (vs $0.15 h^2$ under the lamb–animal + LS model). However, variances were larger for DAB, LWEAN and WEAN in the complete data for lambs, than for the mean values for ewes (Table 3), except when data were constrained to singles (Table 4).

Results for BWT, which is a relatively well recorded trait, demonstrated that estimates of common litter effects for lamb models were high and were also influenced by litter size (models –LS vs +LS). The ratio of this effect (c^2) was typically larger when litter size was not fitted as a systematic effect in lamb–animal models. In both lamb–animal and ewe–sire models, litter size explained approximately 20% of the variation in individual BWT, based on reductions in phenotypic variance (VP), whereas the estimate for c^2 was proportionally larger in lamb–animal models (c^2 0.28). Estimates of c^2 exceeded h^2 for all traits under lamb–animal models. However, only small changes in variance ratios between –LS and +LS models were observed for traits other than BWT. When the common litter effect was not fitted in the model, ratios for all other effects were increased: for BWT by 2% (h_{lamb}^2), 7% (ped^2), 1% (m^2), and 18% (VE/VP). Thus, c^2 effects were repartitioned predominantly to residual variance and the permanent environmental effect of the ewe. The same pattern was observed for all other traits.

In contrast to BWT, with well-defined direct and maternal genetic contributions to trait expression, direct genetic effects for LE, DAB, or survival of lambs were approximately halved in magnitude, with h^2 not exceeding 0.08 under any model, while ratios for maternal genetic effects were about 0.02 if litter size was accounted for. Further, the litter size effect accounted for much less variation in these traits (e.g. DAB, LE, LWEAN or WEAN) than it did for BWT, which is a continuous trait. Analyses for GL failed to converge under the lamb–animal model, whereas GL was moderately heritable as

a trait of the ewe ($h_{\text{ewe}}^2 = 0.21$), and with substantial estimates of sire variance, translating to a direct genetic effect for the lamb of $h_{\text{lamb}}^2 = 0.51$.

Parameter estimates from single litters

Variance ratios for traits recorded from single births were very similar to those obtained with the complete data, which included data from multiple births (Table 4), with the exception that the heritability for LE was very low in this data subset, improving slightly under bivariate analyses for single-born litters (not shown). Ranking of traits on the basis of the magnitude of variance ratios for maternal genetic (m^2 in lamb–animal mode or h_{ewe}^2 in ewe–sire models) or non-genetic (dpe^2 from lamb–animal models or pe^2 from ewe–sire models) effects was essentially equivalent, with similar trait VP across both analyses. However, estimates of heritability for direct genetic effects of lambs were slightly higher under ewe–sire models. Only the ewe–sire analysis converged for GL, and only the ewe–sire model resulted in estimates of heritabilities for LE recorded on singles in these data. However, in a maternal breed, single-born lambs are less representative of the population, which is typified by data from multiple births.

Correlations among traits for single-born lambs

Gestation length had a high positive genetic correlation with BWT, but moderate positive (LE and DAB) or negative (LWEAN or WEAN) genetic correlations with the other traits, suggesting that long GLs were overall detrimental for lambing outcomes. Phenotypic correlations were in the same directions, but much weaker (Table 5).

Genetic correlations of MBS with BWT or GL were negligible, but phenotypically the associations were slightly negative. Genetic correlations of MBS with DAB, LWEAN or

Table 4. Estimates of heritability (h_{lamb}^2 , h_{ewe}^2), common litter effects (c^2), maternal permanent environmental effects (ped^2 , pe^2), maternal genetic (m^2) and service sire effects (ss^2), along with the residual (VE) and phenotypic (VP) variance, from univariate analyses of litters reported with single-born lambs, when analysed as either a lamb (lamb–animal models) or ewe (ewe–sire models) trait.

Trait	N	Mean (s.d.)	Lamb–animal models					Ewe–sire models					
			h_{lamb}^2	dpe^2	m^2	VE	VP	h_{ewe}^2	pe^2	ss^2	VE	VP	* h_{lamb}^2
GL	8705	147.3 (2.54)	FTC	FTC	FTC	–	–	0.19	0.01	0.12	2.54	3.78	0.48
MBS	14 941	2.14 (0.96)	0.02	0.09	0.10	0.524	0.669	0.10	0.13	0.01	0.505	0.664	0.04
BWT	111 323	5.35 (1.10)	0.17	0.08	0.13	0.508	0.824	0.17	0.06	0.05	0.594	0.813	0.20
LE	76 106	1.028 (0.203)	0.004	0.54	0.03	0.019	0.045	0.03	0.23	0.01	0.033	0.045	0.04
DAB	96 005	0.069 (0.254)	0.08	0.04	0.02	0.050	0.058	0.03	0.02	0.03	0.054	0.059	0.12
LWEAN	244 279	0.880 (0.326)	0.09	0.00	0.01	0.079	0.088	0.02	0.02	0.03	0.098	0.104	0.12
WEAN	248 133	0.858 (0.350)	0.09	0.01	0.01	0.093	0.104	0.01	0.01	0.03	0.084	0.088	0.12

Ewe traits are calculated as the average of their lamb records, per litter.

FTC, failed to converge; GL, gestation length (days); MBS, maternal behaviour score (1–5); BWT, birth weight (kg); LE, lambing ease score (1–3); DAB, dead at birth (0 = alive, 1 = dead); WEAN, lamb weaned (0 = not weaned, 1 = weaned); LWEAN, live lamb at birth weaned (0 = not weaned, 1 = weaned); * h_{lamb}^2 , heritability calculated from estimate of service sire variance.

Table 5. Genetic (above diagonal) and phenotypic (below diagonal) correlations between traits, from sire–dam (trait = dam, sire used for additive estimate) vs lamb (trait = lamb) models, from single births.

Trait	Model	GL	MBS	BWT	LE	DAB	LWEAN	WEAN
GL	Ewe–sire	n.a.	0.00 ± 0.17	0.47 ± 0.07	0.18 ± 0.16	0.19 ± 0.10	-0.25 ± 0.09	-0.15 ± 0.10
MBS	Ewe–sire	-0.03 ± 0.03	n.a.	-0.08 ± 0.07	0.33 ± 0.12	-0.13 ± 0.17	-0.20 ± 0.13	-0.28 ± 0.16
BWT	Ewe–sire	0.28 ± 0.01	-0.05 ± 0.01	n.a.	0.37 ± 0.08	0.06 ± 0.05	0.20 ± 0.04	0.32 ± 0.04
	Lamb–animal		n.a.	n.a.	0.62 ± 0.14	0.08 ± 0.04	0.26 ± 0.04	0.16 ± 0.04
LE	Ewe–sire	0.06 ± 0.01	-0.02 ± 0.01	0.14 ± 0.00	n.a.	0.40 ± 0.08	-0.20 ± 0.08	-0.33 ± 0.10
	Lamb–animal		n.a.	0.14 ± 0.00	n.a.	0.45 ± 0.13	-0.03 ± 0.16	-0.31 ± 0.14
DAB	Ewe–sire	0.05 ± 0.01	-0.06 ± 0.01	-0.07 ± 0.00	0.24 ± 0.00	n.a.	-0.81 ± 0.02	-0.63 ± 0.03
	Lamb–animal		n.a.	-0.07 ± 0.00	0.24 ± 0.00	n.a.	0.35 ± 0.05	-0.76 ± 0.02
LWEAN	Ewe–sire	-0.04 ± 0.01	0.01 ± 0.01	0.12 ± 0.00	-0.11 ± 0.00	n.a.	n.a.	0.74 ± 0.83
	Lamb–animal		n.a.	0.12 ± 0.00	-0.12 ± 0.00	n.a.	n.a.	n.a.
WEAN	Ewe–sire	-0.02 ± 0.01	-0.00 ± 0.01	0.12 ± 0.00	-0.17 ± 0.00	-0.42 ± 0.00	0.99 ± 0.01	n.a.
	Lamb–animal		n.a.	0.12 ± 0.00	-0.17 ± 0.00	-0.62 ± 0.00	n.a.	n.a.

Standard errors of 0.00 have s.e. of <0.01. Ewe traits are calculated as the average of their lamb records, per litter.

GL, gestation length (days); MBS, maternal behaviour score (1–5); BWT, birth weight (kg); LE, lambing ease score (1–3); DAB, dead at birth (0 = alive, 1 = dead); WEAN, lamb weaned (0 = not weaned, 1 = weaned); LWEAN, live lamb at birth weaned (0 = not weaned, 1 = weaned).

Significant correlations are highlighted in bold.

WEAN were all negative, implying that higher MBS scores (undesirable) were associated with decreased DAB (desirable), but also decreased lambs weaned. Phenotypic correlations of MBS with LWEAN or WEAN were negligible for single litters.

Moderate (ewe–sire) to high (lamb–animal) positive genetic correlations between BWT and LE (undesirable) were a contrast to the moderate positive genetic correlations of BWT with lambs weaned (desirable), with comparable phenotypic correlations of lower magnitude but consistent direction. Correlations of LE with DAB or lambs weaned were consistently undesirable in direction, as expected. High DAB and high LE had unfavourable correlations with lamb survival traits (LWEAN, WEAN) and were also moderately positively correlated with each other.

Genetic correlations between DAB and lambs weaned (LWEAN or WEAN) were strongly negative under ewe–sire models, as expected. However, under lamb–animal models, the genetic correlation between DAB and LWEAN was positive. No lamb with DAB = 1 had a trait value for LWEAN, such that residual and, therefore, phenotypic correlations were not estimable from single-born litters. The positive estimate of 0.35 between DAB and LWEAN for data solely from single-born litters might reflect the influence of a positive residual covariance, which cannot be estimated.

Correlations among traits for single- and twin-born lambs in tri-variate analyses

The ewe contribution to values for either LE1 or LE2 at each lambing, across multiple lambing events, was fitted

to be the same effect, resulting in a single estimate of maternal genetic or permanent environmental effects for LE. Genetic correlations (r_a) between lambing ease recorded in single versus twin births ranged from 0.20 to 0.33 across tri-variate sire–dam models, suggesting different genetic expression of LE dependent on litter size, but an overall positive association (Table 6). In contrast, under the lamb–animal model, all estimates of the genetic association between LE1 and LE2 were low to moderate and negative (r_a from -0.12 to -0.20).

Genetic correlations between GL and LE scores were moderate and similar for single and twin litters (r_a from 0.18 to 0.38), accompanied by low positive phenotypic correlations (r_p) (r_p 0.03 to 0.06). Genetic correlations between MBS and LE scores did not differ from zero. Genetic correlations between BWT and LE scores were the largest in magnitude for all trait combinations ($r_a \sim 0.50$), and significantly larger for single than for twin births, with higher r_p (0.06 to 0.13) than for GL. Genetic correlations between DAB and LE scores were moderate (r_a 0.15 to 0.36), accompanied by moderate phenotypic correlations (r_p 0.16 to 0.24) and very high correlations between estimates of maternal genetic effects (0.64 and 0.74). The net result for lamb survival outcomes were moderate negative correlations at the genetic and phenotypic levels between LE scores and weaning outcomes, which were of slightly larger magnitude for single births. For all traits but BWT, correlations between maternal genetic effects (column ewe, Table 6) tended to be stronger than correlations between additive genetic effects for lambs.

Table 6. Genetic and phenotypic correlations between LE for single (LE1) and twin (LE2) lambs and each of other traits (T1) in tri-variate analyses, from lamb-animal and ewe-sire models, with common terms for dam covariances for LE.

Trait	Model	Genetic correlations				Phenotypic correlations	
		LE1_LE2	T1_damLE	T1_sireLE1	T1_sireLE2	T1_LE1	T1_LE2
Level		Lamb	Ewe	Lamb	Lamb	Lamb	Lamb
GL	Ewe-sire	0.20 ± 0.13	0.22 ± 0.11	0.38 ± 0.14	0.20 ± 0.13	0.06 ± 0.01	0.04 ± 0.01
	Lamb-animal	-0.18 ± 0.06	0.87 ± 0.47	0.18 ± 0.07	0.27 ± 0.04	0.03 ± 0.01	0.06 ± 0.01
MBS	Ewe-sire	0.22 ± 0.13	0.12 ± 0.11	-0.17 ± 0.18	-0.07 ± 0.17	-0.03 ± 0.01	-0.01 ± 0.01
BWT	Ewe-sire	0.26 ± 0.13	0.32 ± 0.06	0.52 ± 0.07	0.32 ± 0.06	0.12 ± 0.00	0.08 ± 0.00
	Lamb-animal	-0.20 ± 0.06	0.29 ± 0.06	0.50 ± 0.05	0.12 ± 0.03	0.13 ± 0.00	0.06 ± 0.00
DAB	Ewe-sire	0.33 ± 0.13	0.64 ± 0.09	0.15 ± 0.09	0.36 ± 0.07	0.22 ± 0.00	0.20 ± 0.00
	Lamb-animal	-0.12 ± 0.07	0.74 ± 0.09	0.23 ± 0.07	0.22 ± 0.04	0.24 ± 0.00	0.16 ± 0.00
LWEAN	Ewe-sire	0.26 ± 0.13	-0.47 ± 0.09	-0.19 ± 0.08	-0.18 ± 0.07	-0.16 ± 0.00	-0.13 ± 0.00
	Lamb-animal	-0.20 ± 0.06	-0.23 ± 0.13	-0.20 ± 0.07	-0.00 ± 0.04	-0.14 ± 0.00	-0.06 ± 0.00
WEAN	Ewe-sire	0.22 ± 0.13	-0.30 ± 0.11	-0.18 ± 0.09	-0.05 ± 0.08	-0.10 ± 0.00	-0.07 ± 0.00
	Lamb-animal	-0.18 ± 0.07	-0.49 ± 0.11	-0.23 ± 0.07	-0.09 ± 0.04	-0.19 ± 0.00	-0.09 ± 0.00

Significant correlations are highlighted in bold.

GL, gestation length (days); MBS, maternal behaviour score (1–5); BWT, birth weight (kg); LE, lambing ease score (1–3); DAB, dead at birth (0 = alive, 1 = dead); WEAN, lamb weaned (0 = not weaned, 1 = weaned); LWEAN, live lamb at birth weaned (0 = not weaned, 1 = weaned).

Discussion

Lambing ease score versus lamb survival

Lambing ease is a subjective ordinal score, which does not represent evenly spaced intervals quantifying difficulties experienced by ewes and lambs at parturition. Further, LE is scored for both ewes observed and unobserved at lambing, the latter being based on characteristics presented by the ewe or lamb when they are observed post-lambing. Therefore, accuracy of LE scoring is potentially low in field settings. Nevertheless, LE breeding values are included in LAMBPLAN terminal sheep indexes as a strategy to reduce ewe and lamb losses, while limiting antagonistic implications for other production traits (Dehnavi and Swan 2022). The production level (average litter size) of mates (ewes) for rams is known to affect the expression of all of BWT, LE and GL (Li *et al.* 2021) as well as lamb survival (Nel *et al.* 2021). However, models to establish a relative economic value for LE, or to perform genetic evaluation for LE, do not directly account for the combination of effects of litter size on BWT and lamb or ewe survival. The present study disentangled the associations among traits associated with lambing ease and their impact on lamb survival outcomes through accommodating the influence of litter size. The results suggest that the selection emphasis placed on both LE and BWT should differ with litter size of the target population(s).

The presence of multiple births introduces an additional complication compared with analysis of comparable calving-ease data, because litter mates experience a common birth-litter effect known to be important for both offspring birth weight and survival. However, the common litter effect

cannot be properly estimated from small data sets and/or with few lambs per lambing event. Therefore, in this study, the amount of multi-generational data used for parameter estimation was maximised to facilitate sufficient data to estimate c^2 (common litter effects) concurrently with h^2 , rather than using the strategy typically used in other studies of filtering LE data to include only the most informative LE contemporary groups. The latter data filtering dramatically reduces flock-years represented by LE data. Segregating expression of LE by litter size also assisted in the understanding of how genetic evaluation systems for LE could be modified to allow a transition to more direct evaluation of lamb survival, which better accommodates the antagonistic associations between some trait combinations (e.g. BWT and LE vs BWT and survival) and production levels (e.g. litter size), including the complexity introduced by common litter effects.

Lamb survival results from a complicated mix of direct and maternal genetic and non-genetic effects influencing gestation and parturition outcomes, and is also poorly recorded under commercial conditions. Consequently, lambing ease, with an observable association with lamb and ewe losses, supported by small but significant phenotypic correlations in the present study, is the trait that breeders have committed to recording and for which they receive breeding values to aid selection decisions. In both Sheep Genetics (Li *et al.* 2021) and BREEDPLAN analyses (Jeyaruban *et al.* 2016), BWT and GL were the only indirect traits currently used to increase the accuracy of lambing/calving-ease breeding values. Ideally, for sheep, the appropriate emphasis on each of these traits to improve lamb survival outcomes would be better

established through more detailed knowledge regarding their associations with lamb survival outcomes. To that purpose, we obtained estimates of correlations among these traits, along with additional traits such as MBS, and survival traits such as DAB, WEAN and LWEAN. Results from the present study suggest that using DAB data would be advantageous for LE analyses due to moderate genetic correlations between LE and DAB and the higher heritability of DAB than LE in these data. The observation of a DAB lamb is consistent with the description of LE scoring (Sheep-Genetics 2022), which dictates that lambs from an unobserved lambing showing evidence of a difficult lambing are described with a worse score than those from an unobserved lambing resulting in a healthy lamb–ewe combination. Lamb death, represented by DAB records, can be considered as a continuum of a very poor lambing event (Refshauge *et al.* 2016). However, care needs to be taken that DAB, like LE, is scored close to the lambing event and does not systematically represent external factors, such as disease or weather events.

Choice of model and data

The present study used linear models to estimate correlations within an extended set of traits recorded at lambing, or lamb survival, because linear models are robust and easily extended to multi-trait analyses relative to threshold models. Generally, for lamb–animal models, parameter estimates for LE were lower than expected. Previous analyses of LE, BWT and GL (Li and Brown 2016; Li *et al.* 2021) for terminal breeds used much smaller data sets, and were filtered to remove low incidence or less informative contemporary groups for LE. Both phenotypic variance and heritabilities for LE from those studies were generally higher under both linear and threshold models than in the current study. When estimates from the present study are represented on the underlying scale (h_u^2), through $h_u^2 = h_{\text{lamb}}^2 \times (1 - p)/(i^2 p)$ and p is the grouped incidence of 2/3 scores, the range of h_u^2 for LE was from 0.02 to 0.06 under lamb–animal models if all litter sizes were considered.

The present study used LE data, unfiltered for contemporary group incidences, from maternal sheep breeds, resulting in a larger number of records retained for analyses but a lower average incidence of difficult lambings. The lower heritabilities for LE in the present study could result from true population differences between maternal and terminal breeds for LE, and/or the differential filtering of data for LE incidence. Heritabilities for LE1 support the concept that the augmentation approach did not lower LE, because single litters did not have augmented records. Correlations among BWT, GL and LE tended to be slightly lower in magnitude in the present study than other published estimates (Li and Brown 2016; Li *et al.* 2021) but were still within the expected moderate to high values. Very significant differences between terminal and maternal breeds are evident for reproductive level and selection history, which could be expected to

influence outcomes for LE and BWT, for example. Estimates of heritability for LE did not differ substantively between comparable lamb–animal and ewe–sire models, whereas ewe–sire models resulted in increased heritabilities for all other traits. Low heritability of LE in the ewe–sire models supports low heritability for LE generally in these data. This result highlights the general issue of data filtering for genetic evaluation systems, since more informative data may result in higher heritability, but the trade-off is reduced population representation.

The present study also compared lamb- and ewe-level models for all traits. Lamb-level models included some data from lambs with missing dams, whereas dam-level models required dam identity to be known. For single-born litters only, the difference in record numbers per analysis was ~3–5%, but this difference in record number expands when all litter sizes are considered. Therefore, the model comparisons were largely confined to single and twin litters. Unlike the scenario for cattle, where single calves predominate, a lamb-level model must contend with multiple lambs recorded per litter in more prolific breeds. Lamb-level models are not appropriate for MBS or GL. These trait values are recorded at the litter (dam) level, with consequently no variation in the trait value for multiple lambs born within a litter or lambing event. The practical work around for this scenario has been to randomly retain only one record per litter for parameter estimation, including when estimating correlations among traits (Li and Brown 2016), but use all records for lambs when predicting breeding values for individuals (Li *et al.* 2021). This strategy eliminates the need to estimate common litter effects to obtain parameterisation for other sources of covariation, and can facilitate convergence, but relies on sufficient litters for record sampling to be unbiased for these traits. For example, deletion of additional BT or GL records within a litter need to be at random with respect to other traits, which can differ within litters, such as BWT. In the present study, gender was not included in the model for any trait, although it is recognised that gender effects are significant (Li *et al.* 2021). Retaining equivalent models would become complicated when dam phenotypes can reflect single- or mixed-gender litters. Further, lamb gender is not a heritable trait and should generally be well cross-classified for sires, so not fitting gender was not expected to have a substantive impact on results from analyses for the comparisons of interest.

The present study analysing data as lamb traits, in combination with literature from other species, demonstrated that the common litter effect was important for all lamb traits exhibiting within-litter variation. Elevated losses of live-born lamb(s) from litters containing DAB lamb(s) provided additional evidence for a common litter effect on lamb survival. The common litter effect is not typically fitted in the analysis of sheep data due to data structure, whereas accounting for this effect is routine for more prolific species such as pigs. Models fitting the common litter effect demonstrated

that the variance ratio due to litter effects was the largest for all traits (with the exception of the residual), was reduced in magnitude by including litter size in the model, but is also likely to have biased heritability estimates downwards because of sampling covariances between common litter and additive genetic effects (not shown). While fitting a common litter effect in a lamb-level model may be the most biologically meaningful model, sampling covariances among alternative sources of covariation influence the quality of estimates obtained for all parameters, and therefore routinely fitting the common litter effect is not recommended. Accounting for litter size, permanent environmental effects of the dam and/or treating expressions resulting from different litter sizes as different traits are alternative modelling strategies to remove bias in breeding values that could result from otherwise improper parameterisation resulting from the presence of common litter effects in lamb-level models.

Our results also demonstrated that traits such as LE, BWT, or DAB could be analysed as ewe traits with equivalent results. However, variances were similar for the alternative parameterisations only for single-litter data; the complete data set showed larger phenotypic variance for DAB, LWEAN and WEAN in lamb–animal models than in ewe–sire models, *albiet* without gender fitted. Relative to lamb–animal models, ewe–sire level models also reduce the number of random effects from four to three, and make it easier to fit all traits into an ewe-level analysis if desired. Completeness of pedigree, availability of informative lamb-level data and ease of trait integration into multi-trait analyses are also factors to consider for the choice to implement lamb- versus ewe-level models.

Estimates of heritabilities

Estimates of direct heritabilities from ewe–sire models were slightly higher (h^2_{lamb} 0.09) than for lamb–animal models (h^2_{lamb} 0.04) for lamb survival until weaning, whereas ratios for maternal effects were relatively stable across alternative models ($m^2 \sim 0.01$ to 0.03). Nevertheless, when compared within traits, the alternative models were essentially equivalent and resulted in very similar relative ranking of traits for alternative sources of variation, such as direct and maternal genetic effects. For categorical traits or where presence of data on individual lambs for traits (e.g. LWEAN) are conditional on values for other traits (e.g. DAB), or parents have only one phenotype (e.g. WEAN = 1), developing a consensus on parameter estimates through comparisons of the lamb–animal model with an equivalent ewe–sire model is a useful exercise. However, in field data, some caution may be required if sire can be systematically confounded with other factors affecting phenotypes for lambs (e.g. confounding of sires with high lamb losses due to a weather event). Higher estimates of heritabilities from linear models for lamb survival (range 0.03 to 0.07) are reported by [Nel et al. \(2021\)](#) for a small Merino selection line, but maternal genetic effects were not estimable in their data.

Heritabilities in this study were higher than reported by [Brien et al. \(2010\)](#) for lamb survival.

For continuous traits, heritability estimates were generally as expected from the literature. Direct genetic effects for GL were high (h^2_{lamb} 0.51) and consistent in magnitude for single-born lambs, the complete data including litter sizes up to four in the current study, terminal sheep data ([Li et al. 2021](#)) and beef cattle ([Jeyaruban et al. 2016](#)). However, in contrast to cattle, the maternal genetic effect for GL was relatively larger (m^2 0.21), more similar to that reported in other litter-bearing species such as pigs (see review of [Knol et al. \(2022\)](#)). This demonstrates that genetic sources of variation controlling the balance between the time to be born (lamb) and the time to lamb (ewe) alters with an increasing litter size. A similar change in direct versus maternal variance ratios also occurred for BWT and GL, demonstrating that accurate evaluation for both direct and maternal effects is required for these traits in sheep. However, in comparing the same studies, variance ratios for both direct and maternal effects for LE were much lower in sheep than for cattle. This may reflect true species differences, and/or incidence or accuracy of recording for these traits, as well as different population structures, the relative contributions of which to results observed cannot be disentangled.

Single versus multiple litters

Constraining data to single litters only was used to investigate consistency of parameter estimates from lamb–animal and ewe–sire models, because it removes the need to estimate common litter effects explicitly. However, the disadvantage of this constraint is that fewer records are available, both within and across years, and restricting litter size to single-born lambs might change estimated (co)variances due to real biological differences between single and multiple births, which change associations among traits. Further, in maternal breeds, single-born litters are not representative of many lambing events, which result in multiples. Nevertheless, as observed in analyses of the complete data, estimates of variance ratios for direct genetic effects (lamb) tended to be higher in ewe–sire than in lamb–animal models for all traits; estimates of maternal genetic effects were similar for the lamb–animal (m^2) and ewe–sire models (h^2_{ewe}), whereas differences in permanent environmental effects between lamb–animal (ped^2) and ewe–sire models (pe^2) were more variable, due to changes in records from single litters only available per ewe.

Correlations among traits

The adverse genetic correlation between BWT and LE was of a larger magnitude for single-born lambs, ranging from 0.62 in singles-only data (where dpe^2 cannot capture c^2 effectively) to ~ 0.50 when using combined data from singles and twins. The genetic correlations were much lower (<0.32) in twin litters.

This suggests that the effect of joining high BWT sires to more prolific ewes will reduce the implications of high breeding values for BWT on LE. This hypothesis should be tested using further studies. Concurrently, the adverse genetic correlations between LE and LWEAN or WEAN were higher for single-born than for twin-born lambs. These results have implications for the mating of high-BWT terminal sires to commercial ewes, for example, where the expectation of adverse outcomes would be reduced if litter size were higher, at least partly because lamb BWTs are reduced on average with an increasing litter size. However, while dystocia due to large lambs may reduce as litter size increases (Refshaug *et al.* 2016), lambing assistance may still be required due to obstructive interference during lambing, ewe exhaustion, or ewe ill-health (e.g. hypocalcaemia). Thus, poor LE may not solely reflect lamb size, and important contributors may also differ with differing litter sizes.

Poor lambing ease can potentially offset the benefits of higher BWT for offspring survival in affected lambing events. Preliminary analyses confirmed that associations between litter size and BWT were effectively linear, whereas all other associations were non-linear. This suggests that linear models could compromise predictive ability for individual-lamb survival outcomes. In contrast, linear models are also robust across a range of data structures and can still be effective for genetic improvement of categorical traits. The overall relationship between BWT and lambs weaned outcomes was positive, even in multiple-born litters (not shown), supporting the overall concept that higher BWTs are beneficial for offspring-survival outcomes in sheep (Brien *et al.* 2011; Dwyer *et al.* 2016), cattle (Bunter *et al.* 2014) and pigs (Knol *et al.* 2022). In combination, these results suggest that decreasing BWT to avoid LE issues within purebreds with low litter size (e.g. terminal sire breeds) might not be relevant when terminal sires are mated to commercial ewes, and could have detrimental outcomes for commercial lambs weaned, depending on average lamb BWTs in the production environment. This hypothesis could be tested in field data from structured matings. However, this requires head-to-head comparisons of purebred terminal breed matings with terminal \times commercial ewe matings, and also some allowance for differences in heterosis, which may be hard to disentangle.

The accuracy of genetic evaluation for lambing ease could be improved through including DAB as an additional trait in the analysis of LE data. In industry data, recording for DAB tended to be replaced over time by recording LE, or was instead of recording LE. Increased DAB and poor maternal behaviour towards lambs have been demonstrated to accompany lambing difficulties in small studies (Redfearn *et al.* 2023), which may not typically be observed at lambing or reported in the data directly through scoring for LE in field data. Further, an ewe that dies due to lambing difficulties will result in lamb death, even if LE was not observed for lamb(s) within a litter. An ewe experiencing poor LE was also far less likely to

re-appear with further progeny in the data than a dam without LE difficulties recorded, but ewe deaths at or after lambing are not reliably recorded. In contrast, our results suggest accuracies would not be improved by including data on MBS in the analysis of LE.

Adverse relationships between short GL and progeny-survival outcomes have been reported previously for beef cattle (Bunter *et al.* 2014), sheep (Wallace *et al.* 2021) and pigs (Rydhmer *et al.* 2008), where both low BWT and lack of maturity at birth associated with short GL are both problematic for progeny survival. However, the effect of short GL is difficult to avoid in practice, or select against, unless data exist more widely to evaluate genetic differences within progeny of sires for GL. Currently, in sheep, sires are not routinely evaluated for GL, since observations are available only from matings in artificial insemination programs where the conception date is known. Further, genetic parameters indicate that longer GLs will increase all of BWT, the risk of lambing difficulties and lamb DAB. Therefore, GL is a trait with an optimum with respect to lamb survival.

Conclusions

The present study identified that both lambing ease and lamb survival outcomes are lowly heritable traits in field data. While common litter effects were present for traits recorded on lambs, fitting litter size and non-genetic effects of the dam will capture much of this source of variation in lamb-level models, or alternatively lamb data can be averaged per litter and models can be re-parameterised as traits of the ewe. The latter strategy might provide opportunities for some computational advantages in the current recording paradigm, but conversely may not be desirable if additional traits influencing lamb survival become routinely available. The use of records for DAB would increase the accuracy of evaluation for LE and lamb survival traits, whereas maternal behaviour score did not assist in this regard.

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Data availability. Data used in this study can be shared with permission from Sheep Genetics and Meat and Livestock Australia (MLA).

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