Livestock Science 235 (2020) 104007

Contents lists available at ScienceDirect

Livestock Science

journal homepage: www.elsevier.com/locate/livsci

Considerable potential exists to improve lambing performance traits in sheep through breeding

N. McHugh[a,*], T. Pabiou[b], E. Wall[b], K. McDermott[b], D.P. Berry[a]

[a] Teagasc, Animal & Grassland Research and Innovation Centre, Moorepark, Fermoy P61 P302, Co. Cork, Ireland
[b] Sheep Ireland, Highfield House, Shinagh, Bandon P72 ×050, Co. Cork, Ireland

ARTICLE INFO

Keywords:
Sheep
Genetic parameters
Lambing traits

ABSTRACT

The high demand for resources at lambing necessitates strategies to reduce such requirements; one such strategy is breeding programs that enable selection for fewer lambing events requiring assistance as well as less perinatal mortality. The objective of the present study was to estimate the genetic (co)variances for a range of lambing traits in sheep, based on alternative trait definitions that considered differences in mating type and litter size. A total of 158,561 lambing events from both crossbred and purebred Irish sheep were available. Four lambing traits were considered in the analysis: lambing difficulty score, lambing dystocia, lamb perinatal mortality and birth weight. Variance components for each trait were estimated using animal linear mixed models either in the entire data as a whole, or within sub-populations stratified by litter size (i.e., single versus multiple) or stratified by mating type (i.e., crossbred versus purebred animals). The presence of significant re-scaling and re-ranking across population strata were investigated to determine if genotype-by-environmental interactions existed. Considerable genetic variation existed for all lambing traits investigated. Irrespective of the dataset analysed, direct heritability estimates for lambing difficulty score (0.04 ± 0.02 to 0.12 ± 0.03), lambing dystocia (0.04 ± 0.01 to 0.09 ± 0.03), and lamb mortality (0.01 ± 0.01 to 0.09 ± 0.02) were all low. In contrast, lamb birth weight (0.11 ± 0.02 to 0.20 ± 0.04) exhibited a low to moderate direct heritability. Using the entire dataset, the maternal heritability ranged from 0.01 ± 0.005 (lamb mortality) to 0.15 ± 0.02 (birth weight). All direct genetic effects for the lambing traits were positively correlated with each other, except between lamb birth weight and perinatal mortality (-0.15; SE = 0.16). Significantly different genetic variances in different environments and significant re-ranking between environments was detected for lamb mortality (across different mating types and litter sizes), and for lambing difficulty score (only across different litter sizes). Results clearly indicate that ample genetic variation exists for the lambing-related traits investigated.

1. Introduction

The lambing season is one of the most critical periods in sheep production, contributing to productivity and economic returns for the entire production year. The incidence of lamb mortality reported internationally in sheep vary from 8% to 25% (Binns et al., 2002; Maxa et al., 2009; Riggio et al., 2008); this, coupled with high levels of intervention (Dwyer and Bünger, 2012; McHugh et al., 2016) required at lambing, contribute to economic losses as well as associated animal welfare concerns. Hence, a reduction in the requirement for intervention at lambing, as well as a reduction in lamb mortality, is of considerable interest to sheep producers. Farm management practices can mitigate intervention requirements and lamb mortality, but breeding programs may also possibly contribute.

Previous studies have clearly demonstrated evidence of genetic variability in a range of lambing-related traits, including birth weight, lambing difficulty score, and lamb mortality (Everett-Hincks et al., 2014; Li and Brown, 2016; Morris et al., 2000). Such studies, however, have tended to focus on individual breeds and have not attempted to quantify the extent of genotype-by-environment interactions across alternative mating types (i.e., crossbred versus purebred flocks) or litter size. The moderate genetic correlations reported between lamb birth weight and lambing traits (Everett-Hincks et al., 2014; Li and Brown, 2016) suggests that the inclusion of birth weight in multi-trait lambing analyses will improve the accuracy of genetic evaluations for lambing traits.

The objective of the present study therefore was to estimate genetic (co)variance component for a range of lambing-related traits within a

---

[*] Corresponding author.

E-mail address: noirin.mchugh@teagasc.ie (N. McHugh).

https://doi.org/10.1016/j.livsci.2020.104007
Received 24 April 2019; Received in revised form 6 March 2020; Accepted 11 March 2020

Table 1
Number of animals, contemporary groups (CG), flocks (crossbred and purebred), sires, and dams for each trait.

			No. of flocks			
Trait	No of animals	No. of CG	Crossbred	Purebred	No. of sires	No. of dams
Lambing difficulty	35 557	3 041	408	433	2 332	22 080
Lambing dystocia	23 308	1 666	76	354	1 829	15 990
Lamb mortality	53 654	3 269	81	422	2 252	20 135
Lamb birth weight	44 908	2 933	81	310	2 003	15 546

multibreed sheep population, and to quantify the extent, if any, of genotype-by-environment interactions across contrasting mating types (i.e., crossbred versus purebred) and litter size (i.e., single versus multiple). Results from this study will be useful in quantifying the potential gains in lambing performance traits achievable through breeding and whether or not separate genetic evaluations should be undertaken in light of different mating types or ewes differing in prolificacy.

2. Materials and methods

2.1. Data

A total of 158,561 lambing events from 56,889 ewes in 1077 crossbred (64,939 lambing events from 385 flocks) and purebred (93,622 lambing events 935 flocks) flocks in Ireland were available from the years 2011 to 2016, inclusive; 234 flocks had a mixture of crossbred and purebred animals. Four lambing traits, discussed in detail later, were considered in the present study: lambing difficulty score, lambing dystocia, lamb perinatal mortality and lamb birth weight.

In Ireland, lambing difficulty score is recorded by producers for each lambing event on a scale of 1–4 as: 1 = no lambing assistance /unobserved, 2 = slight assistance, 3 = severe assistance and 4 = veterinary assistance (including caesarian). In the present study, lambing difficulty scores were dichotomised into lambing dystocia where ewes requiring severe or veterinary assistance were coded as 1 but ewes recorded as requiring no assistance/unobserved or slight assistance were coded as 0. The ordinal scoring scale for lambing difficulty score was also retained for later analysis. Lamb mortality is recorded by producers based on whether the lamb was alive (mortality = 0) or dead (mortality = 1) within 24 h of birth. For lamb mortality, only flocks that recorded between 2 and 25% lamb mortality annually were retained (n = 26 140 lambs excluded from analysis). Lamb birth weight is recorded by producers using a weighing scale within 24 h of birth; only lambs with a recorded weight at birth between 2 and 9 kg were retained for analysis.

For all lambing traits, records were discarded if the date of birth, flock of birth, dam or sire were unknown; 19 183 lambs were excluded. Only lambs with ≥50% of their breed fraction known were retained; 6655 lambs were excluded. Ewes with no information on parity number were discarded, as were records from ewes of parities >10. Ewe parity was subsequently categorised as 1, 2, 3, 4, or ≥5. Age of the ewe at first lambing was categorised as: 1) lambing between 8 and 18 months of age (i.e., lambing as ewe lambs), or 2) lambing between ≥18 and 28 months of age (i.e., lambing as hoggets). Ewes recorded to have lambed for the first time less than eight months of age were discarded. Litter size was defined as the number of lambs born (alive or dead) per lambing event. Only litter sizes between one (singles) and four (quadruplet) were retained for analysis. As lambing difficulty and dystocia were recorded per lambing event, gender per lambing event was defined as the gender of all lambs combined (McHugh et al., 2017a). For the purpose of investigating the presence of genotype-by-environment interactions, each lamb (event) was categorised as either a purebred or a crossbred; separately all lambs were categorised as being a singleton or multiple.

For all lambing traits, contemporary groups were defined as flock-by-week of lambing, in that flock-mates lambing within the same calendar week in a given year were grouped together. For lambing dystocia, only contemporary groups with at least one recorded incidence of lambing dystocia (i.e., lamb difficulty score 3 or greater) were retained for analysis. For the analysis of genotype-by-environment in litter size, contemporary groups were formed separately for single and multiple bearing ewes; similarly, for lambing traits defined based on mating type, contemporary groups were formed separately for crossbred and purebred ewes within flock. Only contemporary groups with at least five records were retained. The median contemporary group size for the lambing datasets ranged from 14 (lambing difficulty) to 22 (lamb mortality); for contemporary groups formed based on litter size, the median contemporary group size ranged from 9 (single birth weight) to 27 (multiple lambing difficulty); for contemporary groups formed based on mating type the median contemporary group size ranged from 11 (pedigree lambing difficulty) to 18 (commercial birth weight).

Heterosis and recombination loss coefficients for each lamb were calculated as and $1-\sum_{i-1}^{n}\frac{sire_i^2+dam_i^2}{2}$, respectively where sire_i and dam_i are the proportion of breed i in the sire and dam, respectively.

Following all edits, 35 557 lambing difficulty, 23 308 lambing dystocia, 53 654 lamb mortality and 44 908 lamb birth weight records remained. Summary statistics for each trait by litter size and mating type are in Table 1.

2.2. Statistical analyses

Variance components for each lambing trait were estimated using linear mixed models in ASREML (Gilmour et al., 2009) in the whole dataset, but also separately by mating type and by litter size. Fixed effects considered in the models were as reported previously by McHugh et al. (2016); the model employed was:

$$\begin{aligned}\mathrm{Y}_{ijklmnopg} = {} & \mu + \mathrm{CG}_i + \mathrm{Parity}_j{*}\mathrm{AFL}_k \\ & + \sum\nolimits_{l=1}^{8} \beta_l \mathrm{Breed}_l + \mathrm{Het}_m + \mathrm{Rec}_n + \mathrm{Sex}_\mathrm{o} + (\mathrm{NLB}_p) \\ & + \mathrm{Ani}_\mathrm{g} + \mathrm{e}_{ijklmnopg}\end{aligned}$$

where $\mathrm{Y}_{ijklmnopg}$ = lambing difficulty, dystocia, lamb mortality or birth weight, μ = the population mean, CG_i = the fixed effect of contemporary group (flock-by-week of lambing), $\mathrm{Parity}_j{*}\mathrm{AFL}_k$ = the interaction between ewe parity and age at first lambing, $\sum_{l=1}^{8}\beta_l Breed_l$ is the separate regression coefficients for each of the 8 meat breeds, Het_m = the heterosis coefficient of the litter (for lambing difficulty and dystocia) or lamb (for lamb mortality and birth weight), Rec_n = the recombination loss coefficient of the litter (for lambing difficulty and dystocia) or lamb (for lamb mortality and birth weight), Sex_o = the gender of the litter (for lambing difficulty and dystocia) or lamb (for lamb mortality and birth weight), NLB_p = the fixed effect of number of lambs born (included only for lamb mortality and birth weight), Ani_g = random animal direct additive genetic effect; ($\mathrm{N}(0,\mathbf{A}\sigma_g^2)$) and $\mathrm{e}_{ijklmnopg}$ = random residual term ($\mathrm{N}(0, \boldsymbol{I}\sigma_e^2)$).

Each model was progressively built up to include a maternal genetic effect, as well as both a within- and across-litter permanent environmental effect where applicable; a covariance between the direct and maternal genetic components was also estimated. Since the direct and maternal heritability estimated with or without accounting for the covariance between the direct and maternal effect did not differ from each other, only one set of results are reported hereafter. The log-likelihood ratio test between nested models was used to determine whether the addition of extra random terms improved the fit to the data (Ferreira et al., 1999). Genetic correlations were estimated among all lambing traits using the aforementioned model in a series of bivariate analyses.

The presence of genotype-by-environment interactions for each trait in different mating types (i.e., crossbred versus purebred) and in different litter sizes (i.e., single versus multiples) was quantified using bivariate models where each environment was treated as a separate trait. Whether the genetic correlation between the same trait in the different environments differed from unity due to re-ranking was determined by comparing the model log-likelihood of an unconstrained model against a constrained model where the genetic correlation between the same trait in both environments was fixed to unity. In addition, to test for the presence of genotype-by-environment interactions due to re-scaling in the direct additive genetic effect, the log-likelihood of an unconstrained bivariate model was compared to the same model but where the direct genetic variance in both environments was forced to be identical.

2.3. Predictive ability

The ability to predict future lambing performance was used as a measure to validate the estimated breeding values (EBVs) generated using all data combined. All data from the calendar year 2016 were masked. Genetic evaluations in Mix99 (Lidauer et al., 2015) were undertaken using all data available prior to 2016 and EBVs for both the direct effect of each lamb born and the maternal effect of each ewe lambing in 2016 were estimated from the pedigree relationships with the phenotyped animals; the model and variance components fitted were those used in the present study.

For both lambing difficulty score and lamb birth weight, the association with both phenotypes was estimated using a fixed effect linear model in PROC GLM (SAS, 2013) with the respective direct EBV for each lamb born and maternal EBV for each ewe lambing in 2016 both simultaneously fitted as continuous effects in the model. In addition, a separate analysis was undertaken where all fixed effects were fitted simultaneously with the two aforementioned EBVs for both traits. For the binary traits (i.e., lamb mortality and lambing dystocia), the area under the curve (AUC) of the receiver operator characteristic curve (Brubaker, 2008) was used to quantify the probability of correct assignment of lamb mortality or lambing dystocia for the masked data. In addition, the logit of the odds of the lamb surviving or experiencing dystocia were estimated using logistic regression with the direct EBV of the lamb and the maternal EBV of the ewe included as continuous effects in the regression model, and in a separate model with all fixed effects and both EBVs included in the model.

3. Results

The proportion of crossbred and purebred litters ranged from 19 to 29% and from 71 to 84%, respectively in the lambing datasets. The most common breeds represented were: Texel, Suffolk, Charollais and Belclare. Across all the lamb datasets, on average 30.5% of lambs were born as singletons, 56.5% as twins, 12% as triplets and 1% as quadruplets. On average between 12 and 16% of ewes lambed for the first time as ewe lambs across the four lambing datasets.

3.1. Lambing difficulty score

The average lambing difficulty score in the entire dataset was 1.55 but varied from 1.51 for multiple litters to 1.60 for singletons (Table 2). Across the entire dataset the proportion of litters that experienced no lambing assistance or were unobserved was 59%, 29% required slight assistance, 9% required severe assistance and 3% required veterinary assistance. The genetic variance in lambing difficulty scores differed ($P < 0.001$) by litter size with a greater variance associated with singleton lambs; the genetic variance did not differ ($P > 0.05$) between crossbred and purebred animals. The direct heritability in the entire dataset was 0.05 ± 0.01, but ranged from 0.04 ± 0.02 for crossbred lambing events to 0.12 ± 0.03 for singleton-born lambing events (Table 2). The direct heritability for lambing difficulty did not differ by litter size or mating type ($P > 0.05$; Table 2). A maternal heritability (0.03 ± 0.01) was detected in the combined dataset; however, with the exception of lambing difficulty scored on purebred animals, the maternal heritability was not different from zero for all other population strata. The inclusion of an across-litter permanent environmental effect did not improve the model fit to the data. A moderate negative genetic correlation was estimated between the direct and maternal effect (−0.40 ± 0.15) for lambing difficulty score. Strong direct genetic correlations were estimated between lambing difficulty scored on crossbred and purebred lambs (0.76 ± 0.32) and also between lambing difficulty scored on single or multiple litters (0.83 ± 0.05), the latter being different ($P < 0.001$) from unity.

3.2. Lambing dystocia

The incidence of dystocia across the entire dataset was 11.77%% but ranged from 10.44% for multiple lambs to 13.81% for single lambs. The genetic variance did not differ across mating type or litter size ($P > 0.05$; Table 3). Direct heritability for lambing dystocia in the entire dataset was 0.04 ± 0.01, but varied from 0.04 ± 0.02 to 0.09 ± 0.03 depending on the mating type and litter size investigated (Table 3); the direct heritability for lambing dystocia did not differ by litter size or mating type ($P > 0.05$). A small but significant maternal heritability was estimated in the entire dataset (0.02 ± 0.01). No significant across-litter permanent environmental effect was detected. The genetic correlation between the direct and maternal effect was positive and moderate (0.42 ± 0.69), albeit associated with a large standard error.

A weak direct genetic correlation was estimated between dystocia in crossbred and purebred lambs (0.24 ± 0.74), although a large standard error was associated with this estimate. In contrast, the direct genetic correlation between single and multiple recorded lambing

Table 2
Number of records (n), mean (μ) lambing difficulty (scored 1 to 4), genetic SD (σ_g), residual SD (σ_{res}), phenotypic SD (σ_p), direct heritability (h^2_d; standard error in parentheses), and the maternal heritability (h^2_m; standard error in parentheses) for lambing difficulty across all data as well as within litter size and production system.

Item	Trait	n	μ	σ_g	σ_{res}	σ_p	h^2_d (SE)	h^2_m (SE)
All data		35 557	1.55	0.15	0.66	0.68	0.05 (0.01)	0.03 (0.01)*
Litter size	Single	14 029	1.60	0.24	0.67	0.71	0.12 (0.03)	0.00 (0.00)
	Multiple	21 528	1.51	0.16	0.62	0.65	0.06 (0.02)	0.01 (0.01)
Production system	Crossbred	7 882	1.48	0.15	0.69	0.71	0.04 (0.02)	0.02 (0.01)
	Purebred	27 675	1.57	0.16	0.64	0.96	0.06 (0.01)	0.03 (0.01)*

[*] Maternal heritability different ($P < 0.05$) from zero.

Table 3
Number of records (n), mean (μ) lambing dystocia in percentage units, genetic SD in percentage units (σ_g), residual SD in percentage units (σ_{res}), phenotypic SD in percentage units (σ_p), direct heritability (h^2_d; standard error in parentheses), and the maternal heritability (h^2_m; standard error in parentheses) for lambing dystocia across all data as well as within litter size and production system.

Item	Trait	n	μ	σ_g	σ_{res}	σ_p	h^2_d (SE)	h^2_m (SE)
All data		23 308	11.77	0.06	0.29	0.30	0.04 (0.01)	0.02 (0.01)*
Litter size	Single	9 164	13.81	0.10	0.30	0.31	0.09 (0.03)	0.00 (0.00)
	Multiple	14 144	10.44	0.06	0.27	0.28	0.05 (0.02)	0.00 (0.00)
Production system	Crossbred	6 769	11.89	0.06	0.30	0.30	0.04 (0.02)	0.02 (0.02)
	Purebred	16 539	11.74	0.07	0.29	0.30	0.06 (0.01)	0.01 (0.01)

[*] Maternal heritability differed ($P < 0.05$) from zero.

Table 4
Number of records (n), mean lambing mortality (μ) in percentage units, genetic SD in percentage units (σ_g), residual SD in percentage units (σ_{res}), phenotypic SD in percentage units (σ_p), direct heritability (h^2_d; standard error in parentheses), maternal heritability (h^2_m; standard error in parentheses), maternal repeatability (R_m) and the maternal litter (temporary) effect (L_m) for lambing mortality across all animals as well as within litter size and production system.

Item	Trait	n	μ	σ_g	σ_{res}	σ_p	h^2_d	h^2_m	R_m	L_m
All animals		53 654	10.70	0.04	0.27	0.29	0.02 (0.01)	0.01 (0.005)*	0.11 (0.01)*	0.10 (0.01)*
Litter size	Single	11 660	8.39	0.05	0.23	1.03	0.04 (0.03)	0.001 (0.001)	0.04 (0.04)	
	Multiple	41 994	11.34	0.05	0.28	0.30	0.02 (0.01)	0.01 (0.01)*	0.11 (0.01)*	0.10 (0.01)*
Production system	Crossbred	13 810	7.52	0.08	0.22	0.25	0.09 (0.02)	0.001 (0.001)	0.14 (0.01)*	0.14 (0.01)*
	Purebred	39 844	11.80	0.03	0.29	0.30	0.01 (0.01)	0.01 (0.01)*	0.09 (0.01)*	0.08 (0.01)*

[*] Maternal heritability, maternal repeatability and maternal litter effect differed ($P < 0.05$) from zero.

dystocia was moderate (0.53 ± 0.18). Neither correlation was different from unity.

3.3. *Lamb mortality*

The mean incidence of lamb mortality was 10.70% (Table 4) and ranged from 7.52% (crossbred lambs) to 11.80% (purebred lambs). The genetic variance for lamb mortality differed ($P < 0.001$) by mating type but not by litter size, with greater genetic variance associated with crossbred compared to purebred lambs. The direct heritability for lamb mortality in the entire dataset was 0.02 ± 0.01, and ranged from 0.01 ± 0.01 for purebred lambs to 0.09 ± 0.02 for crossbred lambs. The direct heritability estimates for lamb mortality differed by mating type ($P < 0.001$) but not by litter size. A significant maternal heritability was only observed for definitions of lamb mortality that contained large numbers of lambs (i.e., >30 000 records); across all data, the maternal heritability was 0.01 ± 0.005. Significant within- and across-litter permanent environmental variances were detected (Table 4). The genetic correlation between the direct and maternal effect for lamb mortality was 0.15 ± 0.51. A moderate direct genetic correlation was estimated between singleton and multiple lamb mortality (0.44 ± 0.12). A weak direct genetic correlation was estimated between lamb mortality in crossbred and purebred animals (0.05 ± 0.32) albeit with a large associated large standard error. Both correlations differed from unity.

3.4. *Lamb birth weight*

The average lamb birth weight recorded across all data was 4.63 kg and varied from 4.44 kg for multiple lambs to 5.30 kg for singleton lambs. The genetic SD for lamb birth weight was 0.27 kg (Table 5). The genetic variance for lamb birth weight differed ($P < 0.001$) by mating type but not by litter size. A moderate direct heritability for lamb birth weight existed when the entire dataset was considered (0.13 ± 0.01), with the highest direct heritability recorded in crossbred animals (0.20 ± 0.04) which differed ($P<0.001$) by mating type, but not by litter size. A significant maternal variance and within-litter environmental variance was observed for lamb birth weight, and the maternal heritability was similar to the corresponding direct heritability (Table 5). The inclusion of an across-litter permanent environmental effect did not improve the fit of the model. A weak negative correlation was estimated between the direct and maternal effect (−0.20 ± 0.08). The genetic correlations between birth weight measured in crossbred and purebred (0.64 ± 0.12) and between singleton and multiple lambs (0.81 ± 0.02) were strong and, in both incidences, differed from unity. However the genetic correlation between birth weight measured in crossbred and purebred and between singleton and multiple lambs did not differ from 0.80.

3.5. *Correlations among the lambing traits*

Strong positive genetic correlations were estimated between the direct effects for lambing difficulty score and all other lambing traits

Table 5
Number of records (n), mean lamb birth weight in kg (μ), genetic SD in kg (σ_g), residual SD in kg (σ_{res}), phenotypic SD in kg (σ_p), direct heritability (h^2_d; standard error in parentheses), maternal heritability (h^2_m; standard error in parentheses) and the maternal litter (temporary) effect (L_m) for lambing birth weight across all animals as well as within litter size and production system.

Item	Trait	n	μ	σ_g	σ_{res}	σ_p	h^2_d (SE)	h^2_m (SE)	L_m
All animals		44 908	4.63	0.27	0.48	0.77	0.13 (0.01)	0.15 (0.01)*	0.29 (0.01)*
Litter size	Single	9 930	5.30	0.38	0.78	0.93	0.17 (0.05)	0.13 (0.03)*	
	Multiple	34 978	4.44	0.25	0.47	0.74	0.11 (0.02)	0.14 (0.01)*	0.26 (0.01)*
Production system	Crossbred	8 464	4.72	0.38	0.52	0.85	0.20 (0.04)	0.15 (0.02)*	0.31 (0.01)*
	Purebred	36 444	4.61	0.23	0.48	0.75	0.10 (0.02)	0.14 (0.01)*	0.28 (0.01)*

[*] Maternal heritability and maternal repeatability differed ($P < 0.05$) from zero.

Table 6

Genetic correlations (standard error in parentheses) between the direct effects for each trait (above diagonal), the maternal effects for each trait (below the diagonal), as well as the within-trait direct and maternal effect correlations (on the diagonal).

	Lambing difficulty	Lambing dystocia	Lamb mortality	Birth weight
Lambing difficulty	−0.40 (0.15)	0.99 (0.05)	0.62 (0.22)	0.44 (0.12)
Lambing dystocia	0.97 (0.06)	0.42 (0.69)	0.62 (0.27)	0.54 (0.15)
Lamb mortality	0.52 (0.12)	0.71 (0.15)	0.15 (0.51)	−0.15 (0.16)
Birth weight	0.76 (0.08)	0.62 (0.13)	−0.09 (0.07)	−0.20 (0.08)

(Table 6), indicating that lambs that experienced difficult lambings were genetically predisposed to a greater likelihood of death and were also genetically heavier at birth. The genetic correlations between maternal effects for all lambing trait were similar to the respective genetic correlations between the direct effects and were always in the same direction (Table 6).

3.6. Predictive ability

The proportion of the variation in the lambing difficulty score phenotype explained when both the direct and maternal EBVs were included in the model was 6%. The regression coefficient between both the direct and maternal lambing difficulty EBVs and recorded lamb difficulty score in 2016 was 1.16 ± 0.41 for the direct lamb EBV and 1.75 ± 0.49 for the maternal ewe EBV ($P < 0.001$). When all fixed effects were also fitted, the corresponding regression coefficients for direct and maternal EBV were 1.66 ± 0.41 ($P < 0.001$) and 0.25 ± 0.49 ($P > 0.05$), respectively.

For lambing dystocia, the AUC was 0.56 ($P < 0.001$). Results from the logistic regression when only the direct and maternal EBVs were included in the model, revealed that 21% of the lambing events in the top (i.e., worse) 10% predicted probability for lambing dystocia actually experienced dystocia at lambing in 2016, whereas only 12% of lambing events in the bottom 10% predicted probability for experienced dystocia; the corresponding odds ratio of experiencing lambing dystocia was 1.94 times (95% CI: 1.06 to 3.52; $P < 0.01$). When all fixed effects were included in the model along with the corresponding direct and maternal EBV the AUC was 0.61 ($P < 0.001$).

The AUC of the ROC curve for the 2016 masked lamb mortality data was 0.56 ($P < 0.001$). Results from the logistic regression revealed that 17% of lambing events in the top 10% predicted probability for lambing mortality were dead at birth, whereas 4% of lambing events in the bottom 10% predicted probability for lamb mortality were dead at birth; the corresponding odds ratio was 4.78 (95% CI: 1.89–12.04; $P < 0.001$). When all fixed effects for the 2016 masked lamb mortality data was included in the model simultaneously with the direct and maternal EBVs, the AUC was 0.62 ($P < 0.001$).

For lamb birth weight, the proportion of variation explained by both the direct and maternal EBV was 6%. The regression coefficients on lamb birth weight when both the direct and maternal EBV were included in the model were 0.97 ± 0.12 and 0.75 ± 0.09, respectively ($P < 0.001$). When all fixed effect were fitted simultaneously with the direct and maternal EBV, the regression coefficients were 0.28 ± 0.11 ($P < 0.01$) and 0.66 ± 0.07 ($P < 0.001$) for direct lamb EBV and maternal ewe lambing birth weight EBVs, respectively.

4. Discussion

The birth of viable lamb(s) of optimal weight, requiring preferably minimal or no human intervention, is paramount for profitable sheep production. A thorough analysis of lambing traits, whilst accounting for different sub-populations stratified by litter size or mating type, in a large multibreed population of sheep, has not been undertaken to date. Results from this study suggest that ample genetic variation exist for all lambing traits thereby providing a sustainable long-term strategy for improving lambing performance in both the ewe and lamb.

4.1. Genetic parameters

The accurate recording of lambing difficulty score requires close supervision at parturition; therefore lambing difficulty is usually only recorded in intensive indoor lambing systems. Given the nature of the trait, there is a paucity of studies that have investigated the contribution of genetics to lambing difficulty scores or lambing dystocia (Li and Brown, 2016; Macfarlane et al., 2010), relative to the number of studies in cattle (Berry and Evans, 2014; Eriksson et al., 2004; Hickey et al., 2006). The direct and maternal heritability estimated for lambing difficulty score in the present study were, nonetheless, similar to those previously reported in an Australian sheep population (direct = 0.06; maternal = 0.03) by Li and Brown (2016), but lower than the direct heritability (0.20) reported by Macfarlane et al. (2010), although Macfarlane et al. (2010) did acknowledge their estimated direct genetic variance may include a proportion of the maternal genetic effects. Similar direct and maternal heritability estimates were reported in the current study for both lambing difficulty and lamb dystocia, however in all incidences the genetic variance associated with lambing difficulty was greater compared to the genetic variance associated with lamb dystocia. Given the similarity between both traits and the strong genetic correlation observed between lambing difficulty and lamb dystocia, lambing difficulty score rather than lamb dystocia is discussed hereafter. Genetic parameters for lambing difficulty score differed by litter size in the present study, corroborating the results of Li and Brown (2016) who documented the direct heritability for single born lambs to be twice that for multiple born lambs. In the present study the greater direct heritability for lambing difficulty in singles could be attributed to the greater genetic variance (2.30 times greater) compared to multiple born lambs. No previous study has investigated whether heritability estimates for lambing difficulty score differs between crossbred and purebred animals; previous studies have either focused on just a single breed (Macfarlane et al., 2010) or a selection of terminal breeds (Li and Brown, 2016). Results from the current study, however, both in terms of the heritability estimates and the near unity genetic correlations between mating types suggest little evidence of genotype-by-environment effects for lambing difficulty.

Corroborating many previous studies in both sheep (Gama et al., 1991; Morris et al., 2000; Sawhalha et al., 2007) and beef cattle (Eriksson et al., 2004; Meijering, 1984), the direct and maternal heritability estimates in the present study for lamb mortality, irrespective of the dataset evaluated, were low. The low heritability is not unexpected given the plethora of factors that affect lamb mortality. Given the low heritability reported for lamb mortality (Morris et al., 2000), other studies have investigated the genetics of the individual causes of lamb mortality at birth such as starvation exposure, pneumonia or disease (Everett-Hincks et al., 2014; Southey et al., 2004); results on the usefulness of the individual mortality traits in a breeding program were inconsistent across the studies. Information on the potential causes of lamb mortality were not available in the present study. To date, no study has investigated whether the genetic variance for lamb mortality differs by litter size or mating type; results from the present study reveal that the differential in direct heritability estimates was almost ten-fold when comparing crossbred (0.09) and purebred (0.01) lambs, which could be explained by the greater genetic variance recorded in crossbred versus purebred lambs. The greater direct heritability reported in the crossbred lambs may encompass some of the maternal heritability as the maternal heritability in the crossbred population was small (0.001) and did not differ from zero. In contrast to the results from the current study, many previous studies have documented a greater maternal genetic variance for lamb mortality relative to the estimated direct genetic variance (Gama et al., 1991; Sawhalha et al., 2007), although repeated ewe records across years were available, these studies tended not to include an litter environmental effect; therefore (some of) the associated maternal environmental variance may have inadvertently entered the maternal genetic variance

The moderate direct and maternal heritability estimates for lamb birth weight in the present study are in line with previous reported results from sheep populations in Australia (Li and Brown, 2016), Scotland (Riggio et al., 2008) and Canada (Tosh and Kemp, 1994). Previous studies have tended to report greater maternal heritability estimates relative to the reported direct heritability (Riggio et al., 2008; Simm et al., 2002; Tosh and Kemp, 1994), although in these studies, litter-specific environmental effects were not included in the statistical models. A significant across-litter permanent environmental effect was also estimated by Li and Brown (2016) albeit estimates were greater in the present study.

Close to unity negative correlations between the direct and maternal effect are commonly reported for lambing performance traits in sheep (Morris et al., 2000; Southey et al., 2001; Tosh and Kemp, 1994) and calving performance traits in cattle (Eriksson et al., 2004; Meijering, 1984). The estimated correlations between direct and maternal effects within the same trait are, however, highly dependent on the number of records per progeny group (Gerstmayr, 1992) and the data structure; a strong negative correlation may also suggest the presence a of genotype-by-environment interaction (Maniatis and Pollott, 2002). The direct-maternal genetic correlations reported in the current study (-0.40– 0.42) between all lambing performance traits were considerably weaker than previously reported (Eriksson et al., 2004; Southey et al., 2001).

4.2. Genetic correlations among lambing traits

Many studies have identified risk factors associated with lambing traits (McHugh et al., 2016; Morris et al., 2000; Swalha et al., 2007) and in doing so have documented that heavier lambs are more likely to experience a difficult lambing. Furthermore, lambs that experience dystocia have been reported to be more likely to die during or post-parturition (Maxa et al., 2009; McHugh et al., 2016). Therefore, the direction of the genetic correlations between the lambing traits is not unexpected. The strong positive genetic correlation recorded between lamb difficulty score and birth weight indicates that genetically heavier lambs are genetically predisposed to more lambing difficulty. However to ensure unfavourable indirect selection on lighter lamb birth weights, both traits must be recorded and included in a multi-trait breeding objective. Given the moderate to strong genetic correlations reported between the lambing traits in present study, the inclusion of all lambing traits in a multi-trait genetic evaluation will allow for the prediction of more precise estimated breeding values with higher accuracy values especially for traits that are under-recorded (i.e., lambing difficulty).

4.3. Application of results

Genetic evaluations for a given trait assuming equal variance across data sources is most practical, but may not be optimal where significant genotype-by-environment interactions exist. The decision to assume equal variance of a trait across data sources is predominantly a function of the trade-off between practicality and accuracy of genetic evaluations, the latter being a function of the type (i.e., re-ranking or re-scaling) and extent of genotype-by-environment. The accurate reporting of lambing traits, especially lamb mortality and lambing difficulty, by breeders is perceived by some as having a detrimental effect on the estimated genetic merit of their flock and thus the value of their breeding stock (McHugh et al., 2017b). Commercial farmers, however, almost exclusively operate crossbred flocks and engage in breeding programs to aid in the selection of superior performing animals and are therefore less concerned of the impact of genetic evaluations on individual animals. Given such tendencies, it may therefore be preferable to evaluate phenotypes from commercial (i.e., crossbred) flocks as the goal trait for lambing traits and include breeder data as correlated traits. In addition, single versus multiple bearing ewes are generally managed differently pre-lambing and contemporary groups formed based on flock-week of lambing-litter size (single versus multiples) have been shown to yield superior predictive ability compared to contemporary groups formed to include all litter sizes (McHugh et al., 2017a); nonetheless the analysis of McHugh et al. (2017a) assumed that lambing performance for singletons was genetically identical to lambing performance for multiples. Analysis of the genetic variation estimates in the present study revealed that the separation of lamb mortality and lambing difficulty score by mating type yielded different genetic variances indicating that rather than focusing on separate contemporary group definitions as undertaken by McHugh et al. (2017a), separate evaluations may be required for both lamb mortality and birth weight. Despite the sometimes less than unity estimated genetic correlations between the same traits in different environments, Robertson (1959) stated that only traits with a genetic correlation between environments of < 0.80 should be treated as separate traits. Given the moderate to strong correlations recorded for lamb birth weight and lambing dystocia between single and multiple lambs, and between purebred and crossbred, suggests the benefit of separating the lambing traits based on litter size or mating type in the national genetic evaluations is questionable.

Nonetheless, significant re-ranking between environments was detected for lamb mortality (across different mating types and litter sizes), and for lambing difficulty score (across different litter sizes only); this, coupled with the differing genetic variance associated with each trait, suggests the presence of a genotype-by-environment interactions. This indicates that the genetics of lamb mortality and lambing difficulty score should be investigated for single and multiple litters separately and also for purebred and crossbred animals for lamb mortality.

5. Conclusions

Low to moderate heritability estimates, coupled with ample genetic variation, and the availability of routinely collected data on lambing traits clearly indicate that breeding should be strongly considered as a tool to improve lambing performance and reduce labour requirements during the lambing period. This was clearly substantiated by the differential in actual phenotypic lambing difficulty of lambing events, themselves predicted genetically to be divergent for risk of lambing difficulty. There appears to be little evidence of genotype-by-environment at least for the traits and production environments investigated in the present study; the exception was lamb mortality and lambing difficulty score, where some evidence of genotype-by-environment existed.

CRediT authorship contribution statement

N. McHugh: Conceptualization, Methodology, Software, Data curation, Writing - original draft. **T. Pabiou:** Data curation, Writing - review & editing. **E. Wall:** Writing - review & editing. **K. McDermott:** Writing - review & editing. **D.P. Berry:** Visualization, Investigation, Writing - review & editing.

Declaration of competing interest

All authors acknowledge no actual or potential conflict of interest including any financial, personal or other relationships with other people or organizations within three years of beginning the submitted work that could inappropriately influence, or be perceived to influence, their work.

Acknowledgments

This work was supported by the Irish Department of Agriculture, Food and Marine Research Stimulus Fund OVIGEN (14/S/849) and MUTLIREPRO (15/S/696) as well as the H2020 grant SMARTER (No. 772787).

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.livsci.2020.104007.

References

Berry, D.P., Evans, R.D., 2014. Genetics of reproductive performance in seasonal calving beef cows and its association with performance traits. J. Anim. Sci. 92, 1412–1422.

Binns, S.H., Cox, I.J., Rizvi, S., Green, L.E., 2002. Risk factors for lamb mortality on UK sheep farms. Prev. Vet. Med. 52, 287–303.

Brubaker, P.H., 2008. Do not be statistically cenophobic: time to ROC and roll. J. Cardiopulm. Rehabil. Prev. 28, 420–421.

Dwyer, C.M., Bünger, L., 2012. Factors affecting dystocia and offspring vigour in different sheep genotypes. Prev. Vet. Med. 103, 257–264.

Everett-Hincks, J.M., Mathias-Davis, H.C., Greer, G.J., Auvray, B.A., Dodds, K.G., 2014. Genetic parameters for lamb birth weight, survival and death risk traits. J. Anim. Sci. 92, 2885–2895.

Eriksson, S., Nasholm, A., Jonansson, K., Philipsson, J., 2004. Genetic parameters for calving difficulty, stillbirth, and birth weight for hereford and charolais at first and later parities. J. Anim. Sci. 82, 375–383.

Ferreira, G.B., MacNeil, M.D., Van Vleck, L.D., 1999. Variance components and breeding values for growth traits from different statistical models. J. Anim. Sci. 77, 2641–2650.

Gama, L.T., Dickerson, G.E., Young, L.D., Leymaster, K.A., 1991. Genetic and phenotypic variation in sources of preweaning lamb mortality. J. Anim. Sci. 69, 2744–2753.

Gerstmayr, S., 1992. Impact of data structure on the reliability of the estimated genetic parameters in an animal model with maternal effects. J. Anim. Breed. Genet. 109, 321–336.

Gilmour, A.R., Gogel, B.J., Cullis, B.R., Thompson, R., 2009. ASReml User Guide Release 3.0. VSN International Ltd, Hemel Hempstead, HP1 1ES, UK. www.vsni.co.uk.

Hickey, J.M., Keane, M.G., Kenny, D.A., Cromie, A.R., Amer, P.R., Veerkamp, R.F., 2006. Heterogeneity of genetic parameters for calving difficulty in holstein heifers in Ireland. J. Dairy Sci. 90, 3900–3908.

Li, L., Brown, D.J., 2016. Estimation of genetic parameters for lambing ease, birthweight and gestation length in Australian sheep. Anim.l Prod. Sci. 56, 934–940.

Lidauer, M., Matilainen, K., Mantysaari, E., Pitkanen, T., Taskinen, M., Stranden, I., 2015. Technical Reference Guide For MiX99 Solver. Release VIII/2015. Natural Resources Institute Finland.

Macfarlane, J.M., Matheson, S.M., Dwyer, C.M., 2010. Genetic parameters for birth difficulty, lamb vigour and lamb suckling ability in Suffolk sheep. Anim. Welfare 19, 99–105.

Maniatis, N., Pollott, G.E., 2002. Genotype by environment interactions in lamb weight and carcass composition traits. Anim. Sci. 75, 3–14.

Maxa, J., Sharifi, A.R., Pedersen, J., Gauly, M., Simianer, H., Norberg, E., 2009. Genetic parameters and factors influencing survival to twenty-four hours after birth in Danish meat sheep breeds. J. Anim. Sci. 87, 1888–1895.

Meijering, A., 1984. Dystocia and stillbirth in cattle – A review of causes, relations and implications. Livest. Prod. Sci. 11, 143–177.

Morris, C.A., Hickey, S.M., Clarke, J.M., 2000. Genetic and environmental factors affecting lamb survival at birth and through to weaning. N.Z. J. Agri. Res. 43, 515–524.

McHugh, N., Berry, D.P., Pabiou, T., 2016. Risk factors associated with lambing traits. Anim. 1, 89–95.

McHugh, N., Pabiou, T., Wall, E., McDermott, K., Berry, D.P., 2017a. Impact of alternative definitions of contemporary groups on genetic evaluations of lambing traits. J. Anim. Sci. 95, 1926–1938.

McHugh, N., Pabiou, T., McDermott, K., Wall, E., Berry, D.P., 2017b. Impact of birth and rearing type, as well as inaccuracies in recording, on pre-weaning lamb phenotypic and genetic merit for live weight. Translational Anim. Sci. 1, 137–145.

Riggio, V., Finocchiaro, R., Bishop, S.C., 2008. Genetic parameters for early lamb survival and growth in Scottish Blackface sheep. J. Anim. Sci. 86, 1758–1764.

Robertson, A., 1959. The sampling variance of the genetic correlation coefficient. Biometrics 15, 469–485.

Statistical Analysis System (SAS), 2013. SAS User's Guide Statistics. Version 9.4. SASInstitute INC, Cary, NC, USA.

Simm, G., Lewis, R.M., Grundy, B., Dingwall, W.S., 2002. Responses to selection for lean growth in sheep. Anim. Sci. 74, 39–50.

Southey, B.R., Rodriguez-Zas, S.L., Leymaster, K.A., 2001. Survival analysis for lamb mortality in a terminal sire composite population. J. Anim. Sci. 79, 2298–2306.

Southey, B.R., Rodriguez-Zas, S.L., Leymaster, K.A., 2004. Competing risks analysis of lamb mortality in a terminal sire composite population. J. Anim. Sci. 82, 2892–2899.

Sawalha, R.M., Conington, J., Brotherstone, S., Villanueva, B., 2007. Analyses of lamb survival of Scottish Blackface sheep. Animal 1, 151–157.

Tosh, J.J., Kemp, R.A., 1994. Estimation of variance components for lamb weights in three sheep populations. J. Anim. Sci. 72, 1184–1190.