

# Genotype $\times$ birth type or rearing-type interactions for growth and ultrasound scanning traits in Merino sheep

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**Abstract.** This study explores the interaction between genetic potential for growth in Merino lambs and their birth type (BT) or rearing type (RT). Data on birthweight (BWT), weaning weight (WWT), post-weaning weight (PWWT), scan fat (PFAT) and eye muscle depth (PEMD) were used from 3920 single and 4492 twin-born lambs from 285 sires and 5279 dams. Univariate analysis showed a significant sire  $\times$  BT interaction accounting for 1.59% and 2.49% of the phenotypic variation for BWT and WWT, respectively, and no significant effect for PWWT, PFAT and PEMD. Sire  $\times$  RT interaction effects were much smaller and only significant for PEMD. Bivariate analysis indicated that the genetic correlation ( $r_g$ ) between trait expression in lambs born and reared as singles versus those born and reared as twins were high for BWT, WWT, PWWT ( $0.91 \pm 0.02$ – $0.96 \pm 0.01$ ), whereas  $r_g$  for PFAT and PEMD were lower ( $0.81 \pm 0.03$  and  $0.86 \pm 0.02$ ). The  $r_g$  between traits expressed in lambs born and reared as singles versus those born as twins but reared as singles were lower:  $0.77 \pm 0.08$ ,  $0.88 \pm 0.03$ ,  $0.66 \pm 0.06$  and  $0.61 \pm 0.08$  for WWT, PWWT, PFAT and PEMD, respectively. A different RT only affected the expression of breeding values for PFAT and PEMD ( $r_g$   $0.62 \pm 0.04$  and  $0.47 \pm 0.03$ , respectively). This study showed genotype  $\times$  environment interaction for BWT and WWT (sire  $\times$  BT interaction) and for PEMD (sire by RT interaction). However, sires' breeding value of a model that accounts for sire  $\times$  BT interaction provides a very similar ranking of sires compared with a model that ignores it, implying that there is no need to correct for the effect in models for genetic evaluation.

**Additional keywords:** genotype  $\times$  environment interaction, growth traits, univariate and bivariate analysis.

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## Introduction

Genotype  $\times$  environment interaction (GEI) can be defined as genotypes responding differently to changes in the environment (Kolmodin *et al.* 2002; Kolmodin and Bijma 2004). The environment could be described by region, flock, or nutritional management. If the environment varies, the genotypes of animals may respond differently. Different rankings of animals on genetic merit may occur in different environments, or the rankings could be the same but the scale of the expression of genotype differences might vary between environments. When GEI is important, it may be optimal to evaluate and select animals in the appropriate environment (Mulder *et al.* 2006). Alternatively, the genetic evaluation model used to generate estimated breeding value (EBV) should account for such interaction effects (Dominik and Kinghorn 2001; Dominik and Kinghorn 2008; Márquez *et al.* 2015).

Birth type (BT) and rearing type (RT) constitute environmental factors that influence the early life of sheep. Animals born as singles have a better *in utero* environment and have higher birthweight and grow faster than animals born as twins or triplets (de Combellas *et al.* 1980; Thomson

*et al.* 2004; Fogarty *et al.* 2005; Safari *et al.* 2007; Yilmaz *et al.* 2007; Bermejo *et al.* 2010; Oldham *et al.* 2011; Mousa *et al.* 2013). Furthermore lambs reared as singles are heavier than those reared as twins due to the better maternal milk availability (Glimp 1971; Bush and Lewis 1977; Fogarty *et al.* 2005; Safari *et al.* 2007; Huisman *et al.* 2008; David *et al.* 2011). Both BT and RT are likely to continue to influence bodyweight at later age such as weaning weight (WWT) and post-weaning weight (PWWT).

Genotype  $\times$  environment interactions have been studied before in Australian sheep breeding programs, for example for wool and growth traits (e.g. Dominik *et al.* 2001; Carrick and van der Werf 2007) and for parasite resistance (Pollott and Greeff 2004). Swan and Brown (2007) reported that reliability of EBV was improved with inclusion of sire  $\times$  flock-year interaction in the MERINOSELECT data. In this study, we investigated whether the expression of genetic merit depends on or interacts with the BT and RT of lambs. If such an interaction was large, there could be implications for the genetic evaluation, for example there may be a need to account for such interaction in the evaluation model.

The objectives of this study were to estimate genotype  $\times$  BT and RT interactions for bodyweight and ultrasound scanning traits of Merino sheep. These interactions were assessed on variance components and ratios estimated from linear mixed models fitting sire  $\times$  BT or RT interaction effects, as well as based on an estimate of the genetic correlation between expressions of these traits in lambs born and raised as singles or twins.

## Material and methods

Data for this study were obtained from the Information Nucleus program of the CRC for Sheep Industry Innovation in Australia. Details on this program and its design are described by van der Werf *et al.* (2010). Data consisted of birthweight (BWT, kg), weaning weight (WWT, kg), post-weaning weight (PWWT, kg), scan fat (PFAT, mm) and eye muscle depth (PEMD, mm). WWT was measured at  $91.9 \pm 9.5$  days and PWWT, PFAT and PEMD were measured at  $261.1 \pm 43.9$  days of age. Birthweight records were available from 8412 purebred Merino lambs generated from 285 sires and 5279 dams. These sheep were distributed over two BT classes (singles and twins) and two RT classes except for BWT. The lambs were born in eight different flocks between 2007 and 2012 and raised in up to four management groups per flock per year. Details on number of records, and simple trait statistics are presented in Table 1.

Linear mixed models were used for statistical analysis fitting fixed effects of birth year (6 classes), flock (8 classes) and management group within flock as one contemporary group, age of dam (9 classes, 2–10 years), sex (ewes, wethers), age at measurement as a covariate, and BT (single,

twin) and RT (single, twin) as an interaction effect. Additionally, weight at scanning was included as a covariate for PFAT and PEMD.

For each trait, we fitted sire  $\times$  BT, sire  $\times$  RT and sire  $\times$  flock ( $S \times BT = M2$ ;  $S \times RT = M3$ ;  $S \times F = M4$ ;  $S \times BT$  and  $S \times F = M5$ ;  $S \times RT$  and  $S \times F = M6$ ) interactions as a random effect in separate linear mixed models. The models also contained the random effects of animal (additive genetic), dam, and genetic group in a univariate analysis as base model, M1. A pedigree file consisting of 20 010 animals from 11 generations was used. It was assumed that dams were unrelated, hence the dam effect represents both maternal genetic and maternal permanent environmental effects, and relationships among sires were ignored in the  $S \times BT/RT$  interaction terms. There were 135 genetic groups defined according to Merino sub-strain and flock of origin of the base animals (Swan *et al.* 2016). Variance components from all analyses were estimated using ASREML software (Gilmour *et al.* 2009). We used the log-likelihood ratio test (LRT) to compare the model including  $S \times BT$  and  $S \times RT$  with a reduced model to test the significance of the  $S \times BT$  and  $S \times RT$  interaction effect. Heritability estimates were based on the ratio of the additive genetic animal effect and the phenotypic variance, which was the sum of variance components for animal, dam, with and without  $S \times BT$  and  $S \times RT$ , and residual.

In bivariate analyses, we considered a particular trait when expressed in either singles or twins as two different traits and estimated the genetic correlation between the two expressions (Falconer 1952). The magnitude of the GEI was then evaluated based on the value of the estimated genetic correlation. The same model used in the univariate analyses was also used in bivariate analyses, other than omitting the interaction effect, and fitting genetic group, animal and dam as random effects. Traits expression were based on combinations of BT (SS, lamb born and raised as a single; TS, lamb born as a twin and raised as a single; and TT, lamb born and raised as a twin) and used to investigate GEI in an attempt to disentangle effects of BT and RT.

## Results and discussion

### Univariate analyses

Variance components and ratios from all models for the growth and ultrasound traits are shown in Table 2. When  $S \times BT$  interaction was included in the model the heritability estimates decreased for BWT (12.5%) and WWT (31.25%) and for these traits the contribution of  $S \times BT$  was significant. The  $S \times BT$  interaction did not significantly influence PWWT, PFAT and PEMD, and the heritability estimates were similar with and without inclusion of  $S \times BT$  (Table 2). When including  $S \times RT$  in the model, the heritability estimate decreased only for PEMD.

The heritability estimates of BWT ( $0.24 \pm 0.04$ ) without the  $S \times BT$  or  $S \times RT$  interaction effects were slightly higher than heritability estimates reviewed by Safari *et al.* (2005) (with average values of  $0.21 \pm 0.03$  for wool breeds). Heritability estimates of WWT ( $0.16 \pm 0.03$ ) without the  $S \times BT$  or  $S \times RT$  interaction effects were lower than heritability estimates reviewed by Safari *et al.* (2005) (with average values of 0.23

**Table 1.** Summary of simple statistics of the data used for analyses

Traits <sup>A</sup> /BTRT <sup>B</sup>	Number of records	Mean <sup>C</sup>	s.d.	Max.	Min.
BWT (kg) (total)	8412	4.8	1.0	9.0	1.2
S	3920	5.1	1.0	9.0	1.2
T	4492	4.4	0.9	8.7	1.8
WWT (kg) (total)	8302	24.0	4.9	51.2	3.8
SS	3853	25.4	4.8	45.1	8.5
TS	1306	22.7	5.0	51.2	3.8
TT	3143	22.9	4.6	44.2	7.0
PWWT (kg) (total)	7916	37.0	7.7	67.4	20.2
SS	3645	37.2	7.6	67.4	20.2
TS	1223	36.0	7.6	67.2	20.2
TT	3048	37.2	7.9	62.2	20.2
PFAT (mm) (total)	6435	2.4	1.0	9.0	0.5
SS	2957	2.4	1.0	8.0	0.5
TS	901	2.4	1.0	9.0	0.5
TT	2577	2.5	1.1	7.0	0.5
PEMD (mm) (total)	6435	22.7	4.1	42.0	10.0
SS	2957	22.6	3.9	42.0	10.0
TS	901	22.3	3.9	35.0	10.0
TT	2577	23.0	4.3	36.0	10.0

<sup>A</sup>Birthweight (BWT), weaning weight (WWT), post-weaning weight (PWWT), scan fat (PFAT) and eye muscle depth (PEMD).

<sup>B</sup>Birth type and rearing type (BTRT), S (lambs born as a single), T (lambs born as a twin), SS (lamb born and reared as a single), TT (lambs born and reared as a twin), TS (lamb born as a twin but reared as a single).

<sup>C</sup>T-test for mean: TS versus TT for WWT, SS versus TT for PWWT, all combinations for PFAT and SS versus TS for PEMD were not significant ( $P > 0.05$ ).

**Table 2.** Estimates of variance of additive genetic, maternal and sire by birth type and rearing-type effects, heritability and ratios of maternal to phenotypic variance for growth and ultrasound scanning traits in Merino sheep

Traits <sup>B</sup>	$\sigma_a^2$ <sup>A</sup>	$\sigma_c^2$	$\sigma_{(S \times BT(RT))}^2$	$\sigma_{(S \times F)}^2$	$\sigma_e^2$	$h^2$	$c^2$	LRT
BWTM1	0.140	0.182	—	—	0.268	0.24 $\pm$ 0.04	0.31 $\pm$ 0.02	—
BWTM2	0.125	0.185	0.009	—	0.272	0.21 $\pm$ 0.04	0.31 $\pm$ 0.02	7.16
BWTM4	0.120	0.183	—	0.020	0.270	0.20 $\pm$ 0.04	0.31 $\pm$ 0.02	22.8
BWTM5	0.108	0.185	0.008	0.020	0.273	0.18 $\pm$ 0.04	0.31 $\pm$ 0.02	28.46
WWTM1	1.909	2.839	—	—	7.358	0.16 $\pm$ 0.03	0.23 $\pm$ 0.02	—
WWTM2	1.389	2.942	0.302	—	7.491	0.11 $\pm$ 0.03	0.24 $\pm$ 0.02	16.28
WWTM3	1.898	2.842	0.004	—	7.362	0.16 $\pm$ 0.03	0.24 $\pm$ 0.02	0.00
WWTM4	1.476	2.800	—	0.495	7.363	0.12 $\pm$ 0.03	0.23 $\pm$ 0.02	30.24
WWTM5	1.047	2.879	0.287	0.481	7.466	0.09 $\pm$ 0.03	0.24 $\pm$ 0.02	45.00
WWTM6	1.476	2.800	0.000	0.495	7.363	0.12 $\pm$ 0.03	0.23 $\pm$ 0.02	30.24
PWWTM1	7.673	2.850	—	—	16.702	0.28 $\pm$ 0.04	0.10 $\pm$ 0.02	—
PWWTM2	7.207	2.673	0.205	—	16.856	0.27 $\pm$ 0.05	0.10 $\pm$ 0.02	1.62
PWWTM3	7.564	2.600	0.038	—	16.745	0.28 $\pm$ 0.05	0.10 $\pm$ 0.02	0.06
PWWTM4	5.943	2.545	—	1.454	16.972	0.22 $\pm$ 0.04	0.09 $\pm$ 0.02	50.82
PWWTM5	5.797	2.574	0.079	1.444	17.018	0.22 $\pm$ 0.05	0.10 $\pm$ 0.02	51.06
PWWTM6	5.943	2.545	0.000	1.453	16.971	0.22 $\pm$ 0.04	0.09 $\pm$ 0.02	50.82
PFATM1	0.070	—	—	—	0.347	0.17 $\pm$ 0.03	—	—
PFATM2	0.065	—	0.003	—	0.350	0.15 $\pm$ 0.03	—	0.67
PFATM3	0.065	—	0.003	—	0.349	0.16 $\pm$ 0.03	—	0.13
PFATM4	0.054	—	—	0.019	0.345	0.13 $\pm$ 0.03	—	31.67
PFATM5	0.054	—	0.001	0.019	0.345	0.13 $\pm$ 0.03	—	31.71
PFATM6	0.054	—	0.000	0.019	0.345	0.13 $\pm$ 0.03	—	31.71
PEMDM1	1.495	—	—	—	4.239	0.26 $\pm$ 0.03	—	—
PEMDM2	1.439	—	0.004	—	4.262	0.25 $\pm$ 0.04	—	0.00
PEMDM3	1.372	—	0.067	—	4.296	0.24 $\pm$ 0.04	—	3.90
PEMDM4	1.219	—	—	0.277	4.238	0.21 $\pm$ 0.04	—	35.78
PEMDM5	1.217	—	0.002	0.277	4.239	0.21 $\pm$ 0.04	—	35.78
PEMDM6	1.186	—	0.024	0.272	4.254	0.21 $\pm$ 0.04	—	36.18

<sup>A</sup> $\sigma_a^2$ , additive genetic variance;  $\sigma_c^2$ , maternal variance;  $\sigma_{S \times BT}^2$ , sire by birth-type interaction variance,  $\sigma_{S \times RT}^2$ , sire by rearing-type interaction variance;  $\sigma_e^2$  = residual variance;  $h^2$ , direct genetic heritability;  $c^2$ , ratio of dam variance to phenotypic variance.

<sup>B</sup>Birthweight (BWT), weaning weight (WWT), post-weaning weight (PWWT), scan fat (PFAT) and eye muscle depth (PEMD); M1, base model; M2, M1 + S  $\times$  BT; M3, M1 + S  $\times$  RT; M4, M1 + S  $\times$  F; M5, M1 + S  $\times$  BT + S  $\times$  F; M6, M1 + S  $\times$  RT + S  $\times$  F.

$\pm 0.02$  for wool breeds) and heritability estimate reported by Brown and Fogarty (2017) (0.38  $\pm$  0.01).

Heritability estimates of PWWT (0.28  $\pm$  0.04) were slightly lower than heritability estimates reported by Safari *et al.* (2005) for wool breeds (0.33  $\pm$  0.02) and reported by Brown and Fogarty (2017) (0.36  $\pm$  0.01), whereas heritability estimates of PFAT (0.17  $\pm$  0.03) and of PEMD (0.26  $\pm$  0.03) were in the same range as those summarised by Safari and Fogarty (2003) for Merino sheep (0.19–0.26 for SF and 0.24–0.35 for PEMD) and similar with those reported by Brown and Fogarty (2017) (0.13  $\pm$  0.02 for PFAT and 0.26  $\pm$  0.02 for PEMD).

The S  $\times$  BT effect explained 1.59% and 2.49% of the phenotypic variance of BWT and WWT, respectively, for which it was significant. The variance of this interaction component was not much affected by fitting sire  $\times$  flock interaction, i.e. the estimate of  $\sigma_{S \times BT}^2$  differed little between M5 and M2 for the BWT and WWT. The S  $\times$  F interaction component was always significant and generally larger than the S  $\times$  BT interaction. Brown *et al.* (2009) reported a similar pattern with inclusion of a sire  $\times$  flock-year interaction in a model, where 2%, 3% and 4% of variation was explained in

WWT, PWWT and yearling bodyweight of Poll Dorset lambs, respectively, and a large reduction occurred of heritability estimates by up to 50%. In Merino breed, Swan *et al.* (2016) found that sire  $\times$  site interaction explained 3%, 5% and 4% in PWWT, PEMD and PFAT variation, respectively. This is not surprising, given that the heritability estimate is largely based on the variance between half-sib families, which is equal to one-quarter of the heritability (i.e.  $\sim 5\%$  of the phenotypic variance). Maniatis and Pollott (2002) also found that the sire  $\times$  flock-year interaction explained 2–3% of the phenotypic variation in 8-week weight and scanning weight of Suffolk lambs. In data from Merino industry flocks, a sire  $\times$  contemporary group interaction accounted for 2.4% of the variation in bodyweight and 2% and 2–4% of the variation in muscle depth and fat depth (Pollott and Greeff 2004). Mortimer *et al.* (2010) reported, using an earlier sub-set of the data used as in this study with the inclusion of records on maternal breed and terminal sire progeny, that a sire  $\times$  site (flock) interaction effect was significant for WWT, scanning weight, PFAT and PEMD; heritability estimate were 0.14  $\pm$  0.03, 0.27  $\pm$  0.04, 0.15  $\pm$  0.03 and 0.23  $\pm$  0.03, respectively, but estimates of the sire  $\times$  site interaction effects were not given.

The  $S \times RT$  effect was significant for PEMD only, explaining 1.44% the phenotypic variation. The maternal effect contributed to variation in BWT and WWT (31% and 23%), but less so for PWWT (10%). Overall, these results indicate that there is a significant interaction between genotype and BT influencing BWT and WWT.

### Bivariate analyses

Table 3 shows the estimates of genetic correlation between the same traits expressed in lambs where environment was classified according to birth and rearing-type combinations.

Breeding values expressed in an environment of lambs being born and reared as singles versus an environment of lambs being born as twins but reared as a single had genetic correlations between  $0.61 \pm 0.08$  for PEMD and  $0.88 \pm 0.03$  for PWWT. Here, the environment of the lambs differed in BT but the RT was the same. A difference in RT environment for twin-born lambs mainly affected the expression of breeding value for scanned carcass traits, with a genetic correlation of  $0.62 \pm 0.04$  and  $0.47 \pm 0.03$ , PFAT and PEMD respectively. Overall, these results indicate that differences in BT and RT environment experienced by lambs influenced the expression of the growth traits in Merino sheep. Genetic correlations between trait expressions for scanned carcass traits were generally lower. This was expected for PEMD because the  $S \times RT$  interaction was significant, but these results are not consistent with the lack of significant interaction effect we found for PFAT and PEMD in the case of differences in BT. However, note that the number

of lambs in the TS cohort was smaller, especially for the scanned carcass traits, and estimated of variance components for these traits were less accurate. James (1979) pointed out that a relationship exists between the genetic correlation between trait expression in two environments ( $r_g$ ) and the variance component for the interaction between sire and environment ( $\sigma^2_{(S \times E)}$ ) as follows:  $\sigma^2_{(S \times E)} = (1 - r_g) \sigma^2_s$  where  $\sigma^2_s$  is the sire variance, (which is one-quarter of the additive genetic variance). This clearly shows that the interaction component should be lower when the estimated genetic correlation is higher. The relationship holds roughly in our study, with small deviations due to slight differences in data and model.

This study indicated also that different BT environments had a greater effect on the expression of genetic merit in earlier bodyweights ( $0.77 \pm 0.08$  for WWT and  $0.88 \pm 0.03$  for PWWT), whereas different RT environments tended to have a greater effect on later bodyweights ( $0.99 \pm 0.05$  for WWT and  $0.90 \pm 0.02$  for PWWT). In a study where environments were defined by the mean performance of each trait, Carrick and van der Werf (2007) found that differences in genetic expression between more extreme environments were larger for earlier growth traits of sheep with the genetic correlation between the two extreme environments of 0.61, 0.75, and 0.62 for post-weaning weight, PEMD and PFAT for yearling data compared with 0.70, 0.92 and 0.91, respectively, for hogget data. Dominik *et al.* (1999) found that the genetic correlation between breeding values for bodyweight at hogget age in a low and high nutrition group was close to 1,

Table 3. Genetic correlations between growth and ultrasound traits expressed in Merino lambs classified according to birth and rearing-type combinations

Traits <sup>C</sup>	Bivariate analysis <sup>B</sup>				Univariate analysis		
	$rg_{12}$	$h^2_1$	$C^2_1$	$h^2_2$	$C^2_2$	$h^2$	$C^2$
<i>BWT</i>							
$SS \times TT^A$	$0.91 \pm 0.02$	$0.33 \pm 0.06$	$0.22 \pm 0.06$	$0.25 \pm 0.06$	$0.34 \pm 0.05$	$h^2_{SS}, 0.26 \pm 0.05$ $h^2_{TT}, 0.22 \pm 0.05$	$C^2_{SS}, 0.28 \pm 0.04$ $C^2_{TT}, 0.30 \pm 0.03$
<i>WWT</i>							
$SS \times TT$	$0.91 \pm 0.03$	$0.29 \pm 0.06$	$0.27 \pm 0.06$	$0.16 \pm 0.06$	$0.21 \pm 0.05$	$h^2_{SS}, 0.19 \pm 0.05$	$C^2_{SS}, 0.23 \pm 0.04$
$SS \times TS$	$0.77 \pm 0.08$	$0.19 \pm 0.07$	$0.25 \pm 0.07$	$0.10 \pm 0.11$	$0.20 \pm 0.11$	$h^2_{TS}, 0.10 \pm 0.08$	$C^2_{TS}, 0.24 \pm 0.06$
$TS \times TT$	$0.99 \pm 0.05$	$0.10 \pm 0.08$	$0.27 \pm 0.08$	$0.14 \pm 0.03$	$0.22 \pm 0.04$	$h^2_{TT}, 0.12 \pm 0.05$	$C^2_{TT}, 0.22 \pm 0.03$
<i>PWWT</i>							
$SS \times TT$	$0.96 \pm 0.01$	$0.29 \pm 0.06$	$0.06 \pm 0.05$	$0.27 \pm 0.07$	$0.10 \pm 0.04$	$h^2_{SS}, 0.29 \pm 0.05$	$C^2_{SS}, 0.06 \pm 0.04$
$SS \times TS$	$0.88 \pm 0.03$	$0.22 \pm 0.03$	$0.04 \pm 0.05$	$0.16 \pm 0.12$	$0.07 \pm 0.11$	$h^2_{TS}, 0.14 \pm 0.12$	$C^2_{TS}, 0.18 \pm 0.08$
$TS \times TT$	$0.90 \pm 0.02$	$0.20 \pm 0.07$	$0.09 \pm 0.04$	$0.25 \pm 0.07$	$0.07 \pm 0.05$	$h^2_{TT}, 0.27 \pm 0.07$	$C^2_{TT}, 0.08 \pm 0.03$
<i>PFAT</i>							
$SS \times TT$	$0.81 \pm 0.03$	$0.13 \pm 0.05$	—	$0.28 \pm 0.05$	—	$h^2_{SS}, 0.12 \pm 0.05$	—
$SS \times TS$	$0.66 \pm 0.06$	$0.13 \pm 0.05$	—	$0.27 \pm 0.14$	—	$h^2_{TS}, 0.29 \pm 0.14$	—
$TS \times TT$	$0.62 \pm 0.04$	$0.28 \pm 0.13$	—	$0.30 \pm 0.05$	—	$h^2_{TT}, 0.29 \pm 0.05$	—
<i>PEMD</i>							
$SS \times TT$	$0.86 \pm 0.02$	$0.24 \pm 0.05$	—	$0.33 \pm 0.05$	—	$h^2_{SS}, 0.24 \pm 0.06$	—
$SS \times TS$	$0.61 \pm 0.08$	$0.25 \pm 0.06$	—	$0.42 \pm 0.13$	—	$h^2_{TS}, 0.43 \pm 0.13$	—
$TS \times TT$	$0.47 \pm 0.03$	$0.42 \pm 0.13$	—	$0.36 \pm 0.06$	—	$h^2_{TT}, 0.35 \pm 0.06$	—

<sup>A</sup> $SS \times TT$ , correlation between lambs born-reared as single and lambs born-reared as twins;  $SS \times TS$ , correlation between lambs born-reared as single and lambs born as twins but reared as single;  $TS \times TT$ , correlation between lambs born as twins but reared as single and lambs born-reared as twins.

<sup>B</sup> $rg_{12}$ , genetic correlation between trait 1 (for example SS) and trait 2 (for example TT);  $h^2$ , direct genetic heritability;  $C^2$ , ratio of dam variance to phenotypic variance.

<sup>C</sup>Traits include birthweight (BWT), weaning weight (WWT), post-weaning weight (PWWT), scan fat (PFAT) and eye muscle depth (PEMD).



indicating that the different nutritional environments were not influencing the expression of genetic merit in bodyweight of older sheep.

Bodyweight of lambs having twin BT and RT environments (TT) were lower than those with single BT and RT (SS) for BWT and WWT, but their bodyweight were the same for PWWT. In these data, lambs born as twins appear to have undergone compensatory growth post-weaning when the environment is relatively the same between single- and twin-born lambs. This may explain that as a result we observed the expression of genetic merit in PWWT to be essentially the same in lambs of SS and TT birth-rearing combinations. A surprising result is that the genetic correlation between SS and TT environments was much higher than between SS and TS environments, indicating that the rearing type affects the expression of genetic merit significantly when the BT is the same, but less when the BT is different. We did not observe this BT and RT combination in the sire  $\times$  RT interaction variance component, but in the univariate analysis it was more difficult to separate the BT and RT effects. There may be some natural selection effect because lambs in the TS cohort typically will be the surviving sibling in a litter where one lamb died around birth. However, the number of lambs in the TS group was relatively small, so analysis of more data is required for firmer conclusions about separating BT and RT effects.

The existence of GEI could impact on the accuracy of prediction of breeding value and therefore on the effectiveness of a breeding program. The impact of accounting for sire  $\times$  birth-type ( $S \times BT$ ) interaction on the selection of sires can be evaluated by comparing EBV from the various models and compare differences in sire ranking or selection efficiency based on these EBV. We compared EBV on sires for BWT, WWT and PWWT resulting from analysis based on M2 and M1, i.e. with, and without fitting an  $S \times BT$  interaction effect in the model. The results showed that the correlation between EBV from these two models was 0.99, indicating that the impact of accounting  $S \times BT$  interaction on incorrect sire ranking was very small.

## Conclusions

The contribution of sire  $\times$  birth-type interaction to the variation of birthweight and weaning weight was significant, whereas the contribution of sire  $\times$  rearing-type interaction was only significant for eye muscle depth. This study suggested that different BT provided environments influenced early growth potential of lambs (BWT, WWT, PFAT and PEMD), whereas different RT environments influenced the expression of PFAT and PEMD. The prenatal environment appears to have a stronger effect on genetic expression for growth after birth to weaning than the maternal rearing environment. However, we found that a model that accounts for sire  $\times$  birth-type interaction provides a very similar ranking of sires compared with a model that ignores it, implying that there is no need to correct for the effect in models for genetic evaluation.

## Conflicts of interest

The authors declare no conflicts of interest.

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