

Genetic Parameters Revisited for Ultrasound Scanning Traits in Australian Sheep

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ABSTRACT: This study estimated genetic parameters for ultrasound scanning measurements of fat (FAT) and eye muscle (EMD) depths in sheep, expressed during the early post weaning period, from analyses including and excluding body weight (WT) as a covariate and compared these to equivalent genetic parameters derived post analysis. Direct heritability estimates from univariate analyses for all traits were moderate (0.17 to 0.25). Estimates from models with WT adjustment were about 30% higher, while maternal environmental effects were not significant. From bivariate analyses of WT with each of EMD and FAT, genetic variance for WT where EMD and FAT were adjusted was higher than the derived estimates, resulting in increased heritability estimates for WT and negative genetic correlations in comparison to both unadjusted estimates (which were positive) and derived estimates (which were weakly positive). We conclude that the phenotypic adjustment of scanned eye muscle and fat depths to a constant body weight could over-correct the estimated breeding values for these traits and that post analysis adjustment may be a better approach. Adjusting genetic parameter estimates post analysis would allow use of more appropriate models in genetic evaluation.

Keywords: eye muscle depth, fat depth, body weight

Introduction

Ultrasound scanning measurements on live sheep of fat depth and eye muscle depth are key traits used in genetic evaluation schemes world-wide to predict genetic merit for lean meat production. In some of these schemes, such as LAMBPLAN, the genetic evaluation scheme for meat sheep in Australia (Brown et al. 2000), these traits are adjusted for body weight at scanning. This adjustment procedure is used to account for known environmental effects on the performances of animals, which Atkins et al. (1991) had shown to occur in the case of fat depth adjusted for body weight. These authors also showed that the adjustment procedure had the advantage of reducing substantially the influence of maternal effects (age of dam, birth and rearing status) on fat depth, thus potentially removing the need for genetic evaluation schemes to apply further correction of performance records for these influences. Correcting performance records of animals for the influences of identifiable environmental effects is required for accurate genetic evaluation. At the time, these advantages were viewed in the context of a breeding objective of selection for growth rate to a constant weight using a selection criterion of fat adjusted for weight (Atkins et al. 1991), where fatness at a

constant weight was uncorrelated with the equivalent of growth rate to a constant weight, namely weight at constant age. As well, fat depth (Atkins et al. 1991; Brown and Reverter 2002) and eye muscle depth (Brown and Reverter 2002) when adjusted for body weight were shown to be at least as heritable as the unadjusted traits, with the residual covariances of body weight with the adjusted traits estimated to be close to zero.

Despite these advantages, it may be more appropriate to estimate genetic parameters for fat and eye muscle depths from analyses excluding body weights as a covariate. Instead, a multivariate analysis where each trait is appropriately corrected for fixed effects could give unbiased estimates of covariances, and these could be used to derive conditional variances post analysis. Formulae to perform such calculations had been presented by Dodds (1991). van der Werf (2004), in examining the statistical properties of a trait (residual feed intake) that is a linear function of constituent traits (production and feed intake), derived equations to calculate phenotypic and genetic parameters from those of the constituent traits. Genetic evaluation of individual traits without using other traits as a covariate is likely more accurate because each trait can be corrected appropriately for fixed effects and effects of genetic groups, before genetically adjusting them for other traits. The aim of this study was to estimate genetic parameter estimates for ultrasound scanning measurements of fat and muscle depths from analyses including and excluding body weight as a covariate and compare these to genetic parameter estimates for these traits based on conditional variances post analysis.

Materials and Methods

Data. Ultrasound scanning and pedigree records were available from animals generated by the Information Nucleus (IN) program of the Cooperative Research Centre for Sheep Industry Innovation, described by van der Werf et al. (2010). Animals were measured at an average age of 185 d (SD 26.1) for eye muscle depth (EMD) and subcutaneous fat depth (FAT), 45 mm from the midline over the 12th rib, and body weight (WT) at ultrasound scanning. Records were used only from animals that had all 3 traits available (Table 1). The animals were the progeny of terminal (n=6110 progeny), maternal (n=2886 progeny) and Merino sires (n=2022 progeny) mated by AI to Merino and cross-bred (Border Leicester X Merino) ewes at 8 research sites located in 4 Australian mainland states.

Table 1. Summary statistics for body weight (WT, kg), eye muscle depth (EMD, mm) and fat depth (FAT, mm).

Trait	Records	Mean	SD	Range
WT	11,023	41.4	7.8	16.5-78.3
EMD	11,023	25.6	4.8	10.0-45.0
FAT	11,023	2.8	1.1	0.5-8.5

Statistical analyses. The software ASReml (Gilmour et al. 2009) was used to fit an animal model to each trait to estimate parameters from univariate and bivariate mixed model analyses. Fixed effects fitted in all models included: year of birth, site, management group, sire breed, dam breed, sex, birth type, rearing type, age of dam and age at observation (fitted as a covariate) and significant two-way interactions. A fixed effect of genetic group (based on source breed, strain or line of sires and dams) was also fitted. For univariate analyses, as well as fitting a random effect of animal to estimate the additive genetic variance, additional random effects of dam (estimating a maternal effect comprising both maternal genetic and maternal environmental effects), dam x year interaction (estimating environmental variation between litters) and sire x site interaction were fitted to assess their importance in accounting for variation in each trait and identify random effects to be fitted in the bivariate analyses. Log likelihood ratio tests were used to identify the best model for each trait. For each of the combinations of WT with EMD and WT with FAT, bivariate analyses without and with WT fitted as a covariate for EMD or FAT were conducted. Heritabilities and phenotypic and genetic correlations were then estimated from the covariance components. Following equations described by van der Werf (2004) that calculate phenotypic and genetic parameters for a trait that is a linear function of constituent traits from the parameter estimates for those traits, phenotypic and genetic covariances were also derived for WT with each of EMD*, defined as $EMD - z.(WT - \mu_{WT})$ and FAT*, defined as $FAT - z.(WT - \mu_{WT})$ where z is the phenotypic regression from the estimates of bivariate analyses without the WT covariate fitted and μ is the mean for WT.

Results and Discussion

Univariate analyses. Direct heritability estimates for EMD and FAT were moderate from models including WT as a covariate (Table 2) and consistent with mean estimates for these traits (assessed on weaned lambs through to adults) reviewed by Safari et al. (2005), but at the lower end of the range of estimates reviewed by Maximini et al. (2012). The direct heritability estimates were about 30% greater than estimates from models where the WT covariate was excluded. However in the presence of the WT covariate, EMD and FAT were unaffected by maternal permanent environment effects and litter effects. Atkins and Ramsay (2001) also observed an increase in heritability and substantial reduction in the influence of maternal effects on early age expressions of fleece weights in Merino sheep when weaning weight was fitted as a covariate in models used to estimate genetic parameters for these traits.

Table 2. Phenotypic variance (σ^2_p), direct heritability (h^2_d), permanent maternal environment variance (c^2), litter variance (l^2) and sire x site variance (S x F) for early post weaning body weight (WT), ultrasound eye muscle depth (EMD) and fat depth (FAT) estimated without and with WT as a covariate (EMDadj, FATadj) from univariate analyses.

	WT	EMD	FAT	EMDadj	FATadj
σ^2_p [§]	24.3	8.21	0.50	4.89	0.38
h^2_d	0.17	0.19	0.17	0.25	0.22
c^2	0.15	0.03	0.01		
l^2	0.06	0.07	0.07		
S x F	0.05	0.05	0.05	0.05	0.04

[§] Standard errors of estimates: all 0.03 for h^2_d and all 0.02 for c^2 and l^2 .

Bivariate analyses. Across the 3 sets of parameter estimates for WT with EMD and WT with FAT (no WT covariate, with WT covariate and derived from the no WT covariate estimates), phenotypic variances for WT were very similar (Tables 3 and 4). Phenotypic covariances and variances were similar only for estimates where the WT covariate was present and for the derived estimates. The phenotypic correlations of WT with EMD and FAT were strong and positive where these traits were not adjusted, which were higher than the mean literature estimates of 0.36 and 0.33 reported by Safari et al. (2005).

Table 3. Genetic parameter estimates[†] for early post weaning body weight (WT) and ultrasound eye muscle depth (EMD) estimated without and with WT as a covariate for EMD.

	No covariate	Derived [‡]	WT covariate			
Phenotypic (co)variances						
WT	24.35	24.35	24.87			
EMD	8.95	8.20	0.00	4.90	0.16	4.89
Phenotypic correlations						
WT	1.00	1.00	1.00			
EMD	0.63	1.00	0.00	1.00	0.01	1.00
Genetic covariances						
WT	5.22	5.22	7.73			
EMD	1.93	1.87	0.32	1.16	-0.25	1.20
Heritabilities and genetic correlations						
WT	0.21	0.21	0.31			
EMD	0.62	0.23	0.13	0.24	-0.08	0.24

[†] Variances (heritability) on the diagonal, covariances (correlations) below the diagonal.

[‡] Estimates derived from equations of van der Werf (2004) using variances and covariances estimated with no covariate.

Table 4. Genetic parameter estimates[†] for early post weaning body weight (WT) and ultrasound fat depth (FAT) estimated without and with WT as a covariate for FAT.

	No covariate	Derived [‡]	WT covariate			
Phenotypic (co)variances						
WT	24.37	24.37	24.89			
FAT	1.74	0.50	0.00	0.38	-0.22	0.38
Phenotypic correlations						
WT	1.00	1.00	1.00			

FAT	0.50	1.00	0.00	1.00	-0.07	1.00
Genetic covariances						
WT	5.11		5.11		7.77	
FAT	0.36	0.10	0.05	0.07	-0.23	0.09
Heritabilities and genetic correlations						
WT	0.21		0.21		0.31	
FAT	0.52	0.19	0.08	0.19	-0.28	0.23

[†] Variances (heritability) on the diagonal, covariances (correlations) below the diagonal.

[&] Estimates derived from equations of van der Werf (2004) using variances and covariances estimated with no covariate.

Although genetic variances for adjusted EMD and FAT were similar to the derived estimates for those traits, the genetic variance for WT where these traits were adjusted was higher than the derived estimate (7.73 versus 5.22 where EMD was adjusted for WT and 7.77 versus 5.11 where FAT was adjusted for WT). Consequently, heritability estimates for WT from both combinations of traits increased to 0.31 and genetic correlations became negative (-0.08 for WT with EMD and -0.28 for WT with FAT) in comparison to both the unadjusted estimates (estimates greater than 0.5) and the derived estimates (estimates weak and positive). The genetic relationship was weak between WT and adjusted EMD. The pattern of genetic correlation estimates of ultrasound fat and eye muscle depth with body weight being positive from models that did not include WT as a covariate and generally negative from models that did include WT as a covariate was noted by Maximini et al. (2012) in summarizing published literature estimates of the genetic correlation between these traits.

The aim of adjusting ultrasound eye muscle and fat depths for body weight at measurement is to allow selection for composition independent of weight at scanning. The results presented here suggest that phenotypic adjustment of carcass traits is altering the partitioning of variance between effects and overcorrecting the genetic relationship between traits. Another consideration is the fact that the relationships between weight and ultrasound scanning traits change over age such that a quadratic relationship exists, especially when measured at older ages. Post adjustment of the variance components assumes a linear relationship between traits. Further study is required to identify the best method to estimate breeding values for eye muscle and fat depth that appropriately accounts for the environmental effects and genetic groups influencing the traits.

Conclusion

Fitting body weight as a covariate in models used for estimating genetic parameters for ultrasound scanning fat and eye muscle depths in sheep produced genetic covariances among the traits different from those derived from analyses where genetic parameter estimates were adjusted post analysis, leading to increased direct heritability for body weight and negative genetic correlations. Also, adjustment for body weight removed the influence of maternal

effects on these traits observed in univariate analyses and increased direct heritability estimates. Ignoring maternal influences on traits can lead to inaccurate genetic evaluation and prediction of responses to selection from breeding programs. It would then seem more appropriate to derive genetic parameters from models that accounted directly for maternal effects, rather than using a covariate to do so, and then calculate adjusted parameter estimates post analysis. Further studies will examine if these findings apply more generally by estimating genetic parameters under the various models for these traits from later age expressions (post weaning, yearling) and from separate terminal and maternal sire breed data sets.

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