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GENOMIC BREEDING VALUES FOR RESIDUAL FEED INTAKE IN AUSTRALIAN MATERNAL COMPOSITE EWES

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SUMMARY

Residual feed intake (RFI) is difficult to measure, involving either labour-intensive measurements of feed intake and liveweight or specialised equipment, which makes genomic methods ideal for industry-wide selection. We estimated genetic parameters and investigated the accuracy of genomic prediction using five-fold cross-validation, using RFI phenotypes obtained from 465 Maternal Composite ewes measured at post-weaning, hogget and adult ages as a reference population. A genomic relationship matrix was constructed from 37,035 imputed markers. Uni- and multivariate GBLUP for RFI was performed, where records at different ages were either included as repeated measures or treated as separate traits. The first five principal components of the genomic relationship matrix were fitted as fixed effects to account for breed composition. The h^2 of RFI was estimated at 0.19 (±0.04) when all ages were fitted together, and genetic correlations between PW-hogget, PW-adult, and hogget-adult were estimated as 0.29 (±0.28), 0.24 (±0.43), and 0.50 (±0.37), respectively. The accuracy of genomic prediction across all ages was 0.22 (±0.03), and the bias was 1.00 (±0.19). The results suggest that after increasing the training set, breeding values for RFI in the Maternal Composite ewes could be developed.

INTRODUCTION

Feed is the highest cost of sheep production. Subsequently, the sheep industry could potentially increase its profits by selecting for improved feed conversion efficiency (FCE). Residual feed intake (RFI) is the difference between actual and predicted dry matter intake (DMI) required for maintenance, growth, and production (Koch *et al.* 1963) and can be considered to be an indicator of FCE. However, an accurate measurement of DMI of animals at pasture is difficult, and thus RFI testing relies on the measurement of DMI and liveweight gain of intensively housed animals. The process is time-consuming expensive and may require specialised equipment, making it difficult to record at scale on commercial farms. For that reason, RFI is a good candidate trait for improvement through genomic selection.

Genomic selection predicts genomic estimated breeding values (GEBVs) for selection candidates based on their genotype even when their phenotype is unknown (Meuwissen *et al.* 2001). As a reference population, 445 crossed ewes from a population that included Coopworth, East Friesian, Finn, Border Leicester, South African Meat Merino, Texel, Poll Dorset, White Suffolk, Merino, Corridale, NZ Romney and Perendale were recorded for feed intake. Using a common training population usually leads to higher accuracies than using breed-specific reference populations, especially for crossbreeds (Bolormaa *et al*. 2013).

This study estimated genetic parameters and investigated the accuracy of genomic prediction via 5-fold cross-validation for RFI in a reference population of Maternal Composite crossbreds.

MATERIALS AND METHODS

Phenotypes and genotypes. The feed intake and growth rate of 445 Maternal Composite ewes, 251 born in 2013 and 194 in 2014, was obtained using the automated feed intake facility validated

by Muir *et al*. (2020a) at Agriculture Victoria, Hamilton, Victoria (Australia). From the 2013 born ewes, 81 were measured at post-weaning (PW), 195 at hogget, and 218 at adult ages. From the 2014 born ewes, 193 were measured at PW and 189 at hogget ages. At start of the tests, the ewes were 313 (±14), 534 (±19), and 858 (±23) days old at PW, hogget and adult ages, respectively. Animals were adapted to the pelleted diet for 10-14 days before the *ad libitum* feed intake was recorded individually in a group pen with automated feeders. Ewes were distributed across 10 group pens considering a balanced distribution of sires and ewes' liveweights across pens. All sheep were offered hay-based pellets for the duration of feed intake measurements. Pellets had 65% (±2.4) digestibility, 9.8% (±1.6) crude protein, 48% (±3.18) neutral detergent fiber, and 9.6 (±0.58) MJ/kg of dry matter. Feed intake measurements lasted 53 (±3), 42 (±3) and 32 (±0) days for PW, hogget, and adult age ewes, respectively. Live weights were measured three times weekly for the duration of the feed intake measurements. Details of the phenotypes and measurements were reported by Muir *et al.* (2020b).

The animals were genotyped with 12,785, 15,000, or 54,241 single nucleotide polymorphism (SNP) chips and imputed to 38,379 SNPs using Fimpute (Sargolzaei *et al.* 2014). Then, SNPs with minor allele frequency <0.05 were removed, and 37,035 remained for downstream analysis. A genomic relationship matrix (G) was constructed using the function Gmatrix of the R package AGHmatrix (Amadeu *et al.* 2016) using the method of Yang *et al.* (2010).

Residual feed intake. RFI was calculated as the residual DMI after energy sinks and corrected by fixed effects with the expression

Observed DMI = μ + b1ADG + b2MMWT + b3YOB + b4PEN + b5 STAGE + b6AGE + RFI,

where observed DMI is average daily dry matter intake over the measurement period, μ is the overall mean, b1-b6 are partial regression coefficients, ADG is average daily gain (kg/day), MMWT is metabolic mid-weight (kg), YOB is the year of birth, PEN is the pen, STAGE correspond to PW, hogget, or adult, and AGE is the age (days) at the start of the experiment. MMWT was calculated as the average between the liveweight at the start and the final of the test to the power of 0.75. RFI is the residual error of the equation. This model was used to estimate the RFI for the different life stages for all stages together, as preliminary analyses showed that a higher correlation between observed and predicted DMI was obtained when the three life stages were fitted together.

Genomic prediction analysis. Uni- and multivariate genomic best linear prediction (GBLUP) for RFI was performed with the R package ASReml-R (Butler *et al.* 2009). The univariate model fitted the trait at combined PW, hogget, and adult ages as a single trait with repeated measures. Additionally, univariate models for RFI at PW, hogget, and adult as different traits were also conducted. Those distinct traits were also included independently in a multivariate model. The number of records in the models was 876, 274, 384, and 218 for all ages as a single trait, PW, hogget, and adult, respectively. The first five principal components of the genomic relationship matrix were fitted as fixed effects to account for breed composition in all models.

Measurement of accuracy and bias. The accuracy and bias of genomic prediction were estimated for each univariate model using five-fold cross-validation. Initially, the animals were randomly grouped into five cohorts. One of the cohorts was used as a validation cohort by removing its RFI records from the dataset and training with the remaining four cohorts' RFI data and their genotypes. Prediction accuracy was calculated as the Pearson correlation between the GEBVs and the RFI phenotypes. The model bias was assessed as the regression slope of RFI on the GEBV. This was repeated with every validation cohort and averaged across cohorts.

RESULTS AND DISCUSSION

Genetic and phenotypic parameters. The univariate model across all ages resulted in an RFI heritability of 0.19 (±0.04, Table 1). The heritabilities (h^2) at PW was higher in the univariate (0.72 ± 0.21) and multivariate (0.69 ± 0.22) models. The heritabilities of RFI at the hogget age were 0.40

± 0.16 in the univariate and 0.40 ± 0.15 in the multivariate models, consistent with the literature reported for growing animals. Most reported heritabilities of RFI in growing sheep are between 0.17 ±0.07, and 0.45 ±0.08 (François *et al.* 2002; Snowder and Van Vleck 2003; Paganoni *et al.* 2017; Hess *et al.* 2019; Tortereau *et al.* 2020). A lower heritability of 0.11 ±0.05 in growing sheep was also reported by Cammack *et al.* (2005), possibly because their RFI estimation did not adjust for metabolic weight.

Table 1. Heritabilities and genomic prediction accuracies of RFI at PW, hogget, and adult ages

Age	Univariate models			Multivariate model ***		
	h^2 **	Accuracy	Bias	PW	Hogget	Adult
All ages *	0.19 ± 0.04	0.22 ± 0.03	1.00 ± 0.19			
PW	0.72 ± 0.21	0.20 ± 0.19	0.69 ± 1.09	0.69 ± 0.22	0.29 ± 0.28	0.24 ± 0.43
Hogget	0.40 ± 0.16	0.24 ± 0.07	1.05 ± 0.71	0.18 ± 0.06	0.40 ± 0.15	0.50 ± 0.37
Adult	0.35 ± 0.27	0.11 ± 0.16	0.46 ± 1.12	0.00 ± 0.13	0.24 ± 0.07	0.37 ± 0.21

SE in brackets. * Univariate model fitted with RFI at all ages as a single trait with repeated measures. ** h^2 = narrow-sense heritability. *** h^2 in the main diagonal, genetic correlations (upper triangle), and phenotypic correlations (lower triangle).

The heritabilities in adults were 0.35 ± 0.27 and 0.37 ± 0.21 in the univariate and multivariate models, respectively. The heritability in adults being lower than in growing animals is consistent with the literature. In Australia, Merino sheep were measured at PW (n = 1,866), hogget (n = 1,010), and adult (n = 444) ages, with their heritabilities estimated at 0.29 ± 0.08, 0.17 ± 0.07, 0.07 ± 0.08, respectively (Paganoni *et al.* 2017). The heritabilities and their standard error in our study were larger than estimated by Paganoni *et al.* (2017), probably due to the smaller data set in our work.

The correlations had a large standard error, which suggests that the dataset was not large enough to obtain accurate correlations. The phenotypic correlations were 0.18 ± 0.06, 0.00 ± 0.13, and 0.24 ± 0.07 for PW-hogget, PW-adult, and hogget-adult, respectively. Similar correlations between the same ages in Australian Merino were reported, being 0.15 ± 0.03, 0.04 ± 0.05 and 0.33 ± 0.04, respectively (Paganoni *et al.* 2017). With the same population as used in our study, the phenotypic correlation between PW and hoggets born in 2014 was 0.20, and between hogget and adults born in 2013 was 0.17 (Muir *et al.* 2020b). These phenotypic correlations are similar, but not equal to the estimates reported here probably due to the differences in RFI estimation methods and the number of animals included in the analyses derived from the restriction per year Muir *et al.* (2020b) implemented.

The genetic correlation of RFI measured between PW and hogget, PW and adults, and hogget and adults were 0.29 ±0.28, 0.24 ±0.43, and 0.50 ±0.37, respectively. The genetic correlations for the same ages in Australian Merino were 0.36 ± 0.22, 0.00 ±0.53, and 0.75 ±0.74, respectively (Paganoni *et al.* 2017). The higher genetic correlation between hoggets and adults in Paganoni *et al.* (2017) agree with our results. It remains to be confirmed with a larger population whether RFI measurements in lambs are genetically correlated with measurements as adults.

Genomic prediction accuracy and bias. The all-ages single trait model (n = 876) achieved an accuracy of genomic prediction of 0.22 ±0.03, and the bias was 1.00 ±0.19. This model had a lower standard error and was less biased than the univariate models per age. The accuracy of RFI at PW (n = 274), hogget (n = 384), and adult (n = 218) were 0.20 ±0.19, 0.24 ±0.07, and 0.11 ±0.16, respectively and the bias values of those models were 0.69 ±1.09, 1.05 ±0.71, and 0.46 ±1.12, respectively. Adult RFI was less accurate than the other models, which is expected as RFI in adults had higher variance than RFI at PW and hogget ages.

In cattle, genomic selection for RFI is expected to improve feed efficiency, although the reference population size and its relationship to the predicted population are still factors that limit

high reliabilities (Li *et al.* 2020). The reliability (~accuracy^2) of genomic predictions obtained in 3,947 Holstein cows in the USA with a 5-fold cross-validation was 0.34 (Li *et al.* 2020). The same study reported a high RFI reliability in the top 10 sires with most RFI daughters (0.85), but the reliability dropped to < 0.17 in the remaining animals (Li *et al.* 2020). In Australia, GEBVs for RFI were estimated in 4,106 unphenotyped Holstein sires from a reference population of 2,036 individuals obtained with a multi-trait GBLUP model and the reliability was 0.06 ±0.07. (Pryce *et al.* 2015).

CONCLUSIONS

Our results suggest that it is feasible to develop genomic breeding values for RFI in the Maternal Composite ewes. However, expanding the training set is required in order to achieve higher accuracies and to confirm whether RFI in lambs and adults is the same trait.

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