AUSTRALIAN SHEEP BREEDING VALUES FOR WORM EGG COUNT RETAIN PREDICTIVE POWER ACROSS FLOCKS IN THE PRESENCE OF GxE

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SUMMARY

Genotype by environment interactions (GxE) for worm egg count (WEC) in Merino sheep were estimated in eight environments across Australia from the Sheep CRC Information Nucleus flock (IN). Genetic correlations between environments were estimated using a factor analytic model, with mean correlations for each environment ranging from 0.27 to 0.57 for an overall mean of 0.40, confirming the presence of large GxE effects for WEC. The industry genetic evaluation model for WEC fits a direct genetic effect averaged across environments, which is reported back to breeders as the Australian Sheep Breeding Value (ASBV), with a sire by environment interaction term to accommodate deviations in performance (not reported to breeders). This model was validated using the IN data, with results demonstrating that the average genetic effect does retain predictive power across environments, albeit with lower accuracy due to a lower heritability observed in the sire interaction model when GxE effects are large.

INTRODUCTION

Gastrointestinal parasites cause significant economic losses to the Australian sheep industry, and part of the integrated control strategy to reduce these losses is selection of sheep which are resistant to infection (e.g. Eady *et al.* 1996; Gray 1997). The MERINOSELECT and LAMBPLAN across flock genetic evaluation services (Brown *et al.* 2007) provide Australian Sheep Breeding Values (ASBVs) for worm egg count (WEC), and these allow ram breeders to identify genetically resistant sheep. WEC is a highly variable trait and measurements in different environments are affected by a number of different factors, including climatic conditions, worm species, treatment strategies, grazing management and host-parasite interactions. Previous studies based on the MERINOSELECT database have shown significant GxE (Pollot and Greef 2004; Carrick and van der Werf 2007), but are limited by the number of sires used across environments. The Sheep CRC Information Nucleus (van der Werf *et al.* 2010) is an ideal resource to study GxE with a large number of sires progeny tested across eight locations that represent the diversity of Australian sheep production environments. In this study we estimated genetic correlations for WEC across the eight "environments" in the Information Nucleus, and evaluate the impact of significant GxE on the genetic evaluation model used to estimate WEC ASBVs.

MATERIALS AND METHODS

Information Nucleus data description. Worm eggs were counted using a modified McMaster technique and included three species, *H. contortus*, *T. colubriformis*, and *T. circumcincta*. Faecal samples were collected from individual animals when the average of their cohort group exceeded a threshold of 500 eggs per gram (epg). The analyses included 8,509 records from the post-weaning stage (average age 131 days, with a range of 61 to 222 days), collected between 2007 and 2012. The animals represented were the progeny of Merino, Dohne Merino, and SAMM sires mated to Merino dams. They were located at eight sites across Australia and these represent the diversity of

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sheep production environments, and for the purposes of this study sites are defined as environments in the GxE sense. A summary of the numbers of animals and sires represented at each site is shown in Table 1. The total number of sires in the study was 308 and the number of sires used across pairs of sites ranged from 24 to 184. Where available, larval species differentiation by site and year of birth showed that a mixture of *T. colubriformis* and *T. circumcincta* was most common, with *H. contortus* observed in significant numbers only at two sites in a single year for each. WEC data were transferred to the cube root scale for analysis.

Estimation of the genetic correlation between environments. Factor analytic models which are known for the parsimonious description of covariance structures and computational advantages (Meyer 2009) were fitted to the data from all sites using the ASReml software package (Gilmour *et al.* 2009). Fixed effects included contemporary group, formed using management group, site, year, sex, breed type (Merino, Dohne, SAMM) and date of measurement (252 levels), birth type (5 levels: 1-5), rearing type (3 levels: 1-3), age of measurement (in days) fitted as a covariate and dam age (2-10 years) fitted as linear and quadratic covariates. The random sire × site effect was modelled with a factor analytic covariance structure (FA). A model with a single common factor was selected on the basis of the log-likelihood ratio tests. Heterogeneous residual variance was fitted in the model at the site level.

Evaluating the impact of GxE in across-flock genetic evaluations. The MERINOSELECT and LAMBPLAN genetic evaluation systems analyse WEC in a multi-trait model, where the traits are defined by age of measurement in four age stages: weaning, post-weaning, yearling and hogget WEC. For each stage, the model includes a direct additive genetic effect and a sire by flock-year interaction effect. The direct additive genetic effect is reported as the WEC ASBV, while the sire interaction effect is included in the model to account for deviations in performance. These can arise in individual flock-year subclasses due to effects such as GxE, incomplete recording and preferential treatment of sire progeny groups, and is not reported to ram breeders. With this approach, the evaluation model is capable of adjusting for GxE to a degree, such that ASBVs represent an average genetic merit across the environments in which animals are evaluated. Provided the effects of GxE are not too large, it is thought that this is a reasonable approach.

In order to quantify the predictive power retained by WEC estimated breeding values (EBV) in the presence of GxE, we tested this model using a cross-validation procedure using IN post-weaning WEC data. Firstly, we fitted a single trait animal model including a random sire x site interaction term, with fixed effects as described above, to data from seven of the eight sites. We then calculate the regression of progeny performance in the eighth site on the sire EBVs from the seven site analysis, which has an expected value of 0.5. The process was then repeated for all sites.

RESULTS AND DISCUSSION

The results from univariate analyses for each site show that mean $WEC^{0.33}$ was considerably higher for Kirby and Turretfield (>10 $epg^{0.33}$) than the other sites which averaged 7.3 $epg^{0.33}$ (Table 1). Phenotypic variances also differ significantly across sites, ranging from 3.42 for Rutherglen to 8.34 for Struan. Heritability estimates were low to moderate across sites, ranging from 0.05 ± 0.11 for Hamilton to 0.58 ± 0.07 for Katanning. Generally low to moderate genetic correlations were observed across sites, with the mean correlation for each site with all other sites varying from 0.27 to 0.57 (Table 1), and correlations between individual pairs of sites ranging from 0.21 to 0.85 (not shown). Although the standard errors of genetic correlation estimates were comparatively high due to the relatively small dataset, the mean estimates for each site with all other sites shown in the last column of Table 1, were significantly lower than 0.8 for four out of eight sites. With 0.8 the commonly accepted threshold considered to show biological importance (Robertson, 1959), the results confirm the presence of significant GxE for WEC. This is consistent with two other studies on GxE in Merinos (Pollot and Greef 2004; Carrick and van der Werf 2007). One of the alternative

methods to account for GxE in the genetic evaluation system is the multiple-trait MACE method (Schaeffer, 1994). However, the main difficulty for this trait is how to classify environments, given that there is no obvious pattern in this dataset in terms of the associations between the extent of genetic correlation and geographical or climatic information (results not shown).

Table 1. Number of records, sires, mean of WEC$^{0.33}$, and estimates of the phenotypic variance (V_p), heritability (h^2), and mean GxE genetic correlation (r_g) between environments at each site. Standard errors in brackets (s.e.)

Site	Location	Records	Sires	Mean	V_p (s.e.)	h^2 (s.e.)	Mean r_g (s.e.)[A]
1	Kirby NSW	2482	296	10.8	8.16 (0.24)	0.22 (0.05)	**0.36** (0.19)
2	Trangie NSW	672	69	6.0	4.97 (0.28)	0.21 (0.08)	0.46 (0.25)
3	Cowra NSW	575	89	6.9	6.20 (0.38)	0.21 (0.10)	0.49 (0.26)
4	Rutherglen VIC	845	106	7.7	3.42 (0.18)	0.26 (0.08)	0.39 (0.21)
5	Hamilton VIC	507	71	8.3	4.49 (0.29)	0.05 (0.11)	0.57 (0.23)
6	Struan SA	721	103	6.6	8.34 (0.47)	0.27 (0.11)	**0.31** (0.22)
7	Turretfield SA	1066	110	10.6	5.38 (0.25)	0.31 (0.07)	**0.31** (0.18)
8	Katanning WA	1641	196	8.0	5.85 (0.23)	0.58 (0.07)	**0.27** (0.14)
Mean		1064	130	8.1	5.85	0.26	0.40

[A]Genetic correlation estimates in bold are significantly less than 0.8 at p=0.05 level.

Cross-validation results are shown in Table 2, and on average the regression of offspring performance on sire EBVs calculated in other environments was exactly 0.5, although there was a large range (0.33 to 0.81). This demonstrates that EBVs from a genetic evaluation model fitting sire interaction effects do have predictive power across environments in the presence of significant GxE. We note however that when compared to the average within-environment heritability estimate (0.26 in Table 1), heritability estimates were significantly lower from the single trait sire interaction model fitted across sites (0.09 in Table 2). This can be interpreted by extension of the co-heritability concept from the theory of correlated response (e.g. Falconer and Mackay, 1996): the co-heritability for selection in environment X targeting response in environment Y can be viewed as $\boldsymbol{h_X h_Y r_g}$ where $\boldsymbol{h_X}$ and $\boldsymbol{h_Y}$ are the square roots of heritability in each environment and $\boldsymbol{r_g}$ is the GxE genetic correlation between environments. With an average heritability of 0.26 and average GxE genetic correlation of 0.40 from the results shown in Table 1, the co-heritability has an approximate value of 0.10 in these data. This is very similar to the average heritability estimate shown in Table 2. So while these results show that WEC ASBVs from MERINOSELECT and LAMBPLAN are likely to have predictive power across flocks even in the presence of significant GxE, they will have lower accuracy in an across flock context. For a co-heritability of 0.10 and within environment heritability of 0.26, the reduction in accuracy based on own performance is approximately 38% (calculated from $\sqrt{0.10}/\sqrt{0.26}$). For progeny-tested sires the reduction in accuracy will be lower as the number of progeny increases, especially if these progeny are represented across different environments.

The MERINOSELECT model for post-weaning WEC assumes a heritability of 0.2 and a sire x site interaction variance ratio of 0.02, considerably different to the average estimates of 0.09 and 0.06 of the same parameters in Table 2. It is likely that the difference is due to data structure: in the IN data the majority of sires are used across sites, whereas in the MERINOSELECT data for approximately 60% of the sires that have progeny with WEC measurements, the progeny were recorded in one flock only, and so GxE effects are not represented in a large part of the data.

Table 2. Cross-validation results for each environment, where V_p (phenotypic variance), h^2 (heritability), and s^2 (sire by site interaction variance ratio) are estimated from a single trait analysis of data for all sites *excluding* the site shown in each row, and b is the regression of offspring performance at the site shown in each row on sire EBVs calculated from all other sites. Standard errors in brackets (s.e.)

Site	Location	V_p (s.e.)	h^2 (s.e.)	s^2 (s.e.)	b (s.e.)
1	Kirby NSW	5.70 (0.12)	0.10 (0.03)	0.07 (0.01)	0.81 (0.19)
2	Trangie NSW	6.56 (0.12)	0.09 (0.02)	0.06 (0.01)	0.33 (0.17)
3	Cowra NSW	6.46 (0.12)	0.09 (0.02)	0.06 (0.01)	0.66 (0.21)
4	Rutherglen VIC	6.76 (0.13)	0.08 (0.02)	0.06 (0.01)	0.39 (0.14)
5	Hamilton VIC	6.55 (0.12)	0.07 (0.02)	0.07 (0.01)	0.63 (0.21)
6	Struan SA	6.30 (0.12)	0.10 (0.02)	0.06 (0.01)	0.33 (0.20)
7	Turretfield SA	6.60 (0.13)	0.09 (0.02)	0.06 (0.01)	0.33 (0.13)
8	Katanning WA	6.54 (0.13)	0.08 (0.02)	0.04 (0.01)	0.53 (0.12)
Mean		6.43	0.09	0.06	0.50

The data used in this study have also been used to develop genomic predictions which are used in the calculation of WEC ASBVs. For Merinos the accuracy of these genomic predictions is estimated to be 0.26 (Swan *et al.*, 2014). The genomic analyses are based on IN data from all sites, and it would be worthwhile to investigate the impact of GxE on these analyses.

CONCLUSIONS

The results presented demonstrate that there are significant GxE for WEC in Merino sheep, but that the analysis method used in industry genetic evaluations can account for these to a degree. Although the accuracy of breeding values is most likely to be lower in an across flock context, ram breeders can have confidence in ASBVs based on performance data collected in their own flocks, and for sires with large numbers of progeny tested across a range of environments.

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