AN ACROSS-FLOCK ANALYSIS ON FAECAL WORM EGG COUNTS IN MERINO SHEEP IN SOUTH AFRICA

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SUMMARY

Previous South African studies on faecal worm egg count (FWEC) in South African Merinos have been limited to analyses within flocks. This study details an across-flock-season analysis of FWEC at the Tygerhoek and Elsenburg research farms using 9080 records collected between 1995 and 2016. Two discrete environments were identified, namely an autumn lambing season at Tygerhoek, and a winter lambing season at Elsenburg. The exchange of sires across environments allowed the estimation of the sire x site variance as an indication of a genotype x environment interaction for FWEC. At 0.12 ± 0.02, FWEC was lowly heritable across environments. Additionally, variance ratios for the dam permanent environment and sire x site contributed respectively 0.03 ± 0.01 and 0.014 ± 0.006 to the observed phenotypic variation. Selection for a reduced FWEC across flocks would likely result in genetic gains, while the probability of a major reranking of sires across sites appears to be small.

INTRODUCTION

So far, research in South Africa has focused on deriving genetic parameters for faecal worm egg count (FWEC) and on correlations of FWEC with other traits of economic importance within flocks or localities. For FWEC to be considered as an indicator of resistance to round worm infection in South Africa (as advocated by Cloete *et al*. 2014) it is important to conduct analyses across flocks. Across-flock analyses allow for the estimation of genotype x environment interactions (G x E; van Wyk *et al*. 2008). Such analyses became commonplace for FWEC in other sheep producing countries such as Australia (Brown *et al*. 2016; Brown and Fogarty 2017) and New Zealand (Pickering *et al*. 2012). Sheep farmers in these countries are thus benefiting from advances brought about by using across-flock genomic breeding values for FWEC for the selection of replacements with resistance to gastro-intestinal nematodes. South Africa has been lagging with respect to these advances. This study, therefore, reports the first across-flock analysis for FWEC in South African sheep. Linkage provided by sires across flocks additionally allowed the estimation of the sire x flock/season variance as an indication of G x E as hypothesized for FWEC.

MATERIALS AND METHODS

The study combined data from Merino flocks maintained on the Tygerhoek and Elsenburg research farms. Both farms are situated in the Mediterranean region of South Africa, Tygerhoek at 34˚08’ S and 21˚11’ E and at an elevation of 425 m. Elsenburg is located at 33˚51’ S and 18˚50’ E, at an elevation of 177. Rainfall averages 425 mm at Tygerhoek and 606 mm at Elsenburg, with respectively 60% and 77% of the precipitation recorded from April to September (Cloete *et al*. 2016). The management, breeding and husbandry of both flocks are well described (Tygerhoek: Cloete *et al*. 2007; Elsenburg: Mpetile *et al*. 2015). Further information on these topics will thus be omitted. Faecal grab samples were obtained from the rectum of individual sheep and counted at an accuracy of 100 eggs per gram (epg) wet faeces at the Regional Veterinary Laboratory at Stellenbosch. Worm challenge at the respective localities was not quantified, but Cloete *et al*. (2016) suggested that a mixed challenge of *Teladorsagia* spp, *Trichostrongylus* spp and *Nematodirus* spp

was more likely at Tygerhoek. A greater reliance on irrigated pastures at Elsenburg resulted in hematophagous parasites like *Haemonchus contortus* becoming more important (Cloete *et al*. 2016). Data at Tygerhoek were recorded from 1995 to 2016, except for 2004 when no data were available (Cloete *et al*. 2007). The data at Elsenburg were recorded over the same period, except for 1997 to 1996 and 2000 (Mpetile *et al*. 2015). Flock data at Tygerhoek and Elsenburg contributed respectively 6,527 hogget and 2,563 yearling records to the study. Age at recording (± s.d.) was 498 ± 38 days at Tygerhoek and 322 ± 30 days at Elsenburg.

Mpetile *et al*. (2017) reported that season had a profound effect on genetic variation of FWEC at Tygerhoek, with the heritability of FWEC using spring samples being substantially higher than for samples collected in autumn. As lambs were born in autumn at Tygerhoek and winter at Elsenburg, samples for FWEC were taken during spring at Tygerhoek and autumn at Elsenburg. This seasonal effect was confounded with location, but eight sires with progeny at both locations and having, on average, 40 ± 12 recorded offspring at Tygerhoek and 17 ± 5 recorded offspring at Elsenburg linked the data recorded on the two locations.

Given the well-established deviations from normality in FWEC data, individual records were transformed to natural logarithms after 100 was added to account for zero counts. Previous studies on the respective resource flocks also tested the cube root transformation at Tygerhoek (Cloete *et al*. 2007) and Elsenburg (Mpetile *et al*. 2015). Genetic parameters stemming from the alternative approaches did not differ and the analysts preferred the log transformation for its lower coefficient of variation. The data so derived were analysed by single-trait analyses using ASREML (Gilmour *et al*. 2015). Fixed effects fitted included contemporary group (90 levels involving year-site-season-sex combinations), age of dam (2-6+ years) and birth type (single vs. multiple). Random effects were sequentially added to the fixed-effects analysis as described in Table 1.

Likelihood Ratio tests (LRT) were used to test the significance of random effects. A random effect was considered significant when its inclusion in the model improved the log likelihood ratio using the Chi^2 distribution as a test statistic. When models had the same number of random effects, the model with the highest log likelihood was preferred. After the the most appropriate model was determined, the random effect of sire x site (encompassing 566 levels) was added to the model by fitting an identity matrix linking sire x site effects to the data (see Table 1). The LRT was then conducted additionally to assess this effect for significance. Phenotypic variance was expressed as the total of all the estimated variance components. Variance ratios were derived by dividing significant ($P < 0.05$) variance components by the phenotypic variance. The pedigree file used in all analyses contained 14832 animals, the progeny of 830 sires and 4342 dams.

RESULTS AND DISCUSSION

The raw data were leptokurtic and skewed with extreme individual variation of FWEC records ranging from 0 to 32700 epg of wet faeces and an overall mean of 1960 ± 2599. The log transformation improved the distribution of the data appreciably resulting in a normal distribution (skewness = -0.32; kurtosis = -0.58) and a coefficient of variation of 17.9% with a mean of 6.97 ± 1.25. These results were consistent with previous studies on these flocks (Cloete *et al*. 2007; Mpetile *et al*. 2015) and are not discussed. Contemporary group exerted a marked effect on the data ($P < 0.001$), while FWEC depended less on age of dam ($P = 0.57$) and birth type ($P = 0.07$).

The LRT suggested that the log likelihood improved markedly from a model consisting of only fixed effects to a model including additive genetic effects (Table 1). Compared to this model with only one random effect, the addition of maternal additive effects did not result in an improvement ($P > 0.05$). Adding dam permanent environmental (PE) effects improved the log likelihood, though. Including both maternal genetic and PE effects did not change the log likelihood when added to the latter model. Adding the sire x site variance to the model including additive and dam PE effects resulted in a further improvement in the log likelihood.

Table 1. Log likelihood ratios for the various models fitted in the across-flock analysis conducted on the Tygerhoek and Elsenburg Merino flocks (Chi² values are for the more comprehensive model compared to the simpler model with 1 less random effect)

Effect fitted	Random effects	Log likelihood value	#Chi²
Fixed effects (FE) only	0	-3708.39	NA
FE + σ^2_a (Model 1)	1	-3641.62	133.54**
FE + σ^2_a + σ^2_m (Model 2)	2	-3640.21	2.82ns
FE + σ^2_a + σ^2_{pe} (Model 3)	2	-3637.75	7.74**
FE + σ^2_a + σ^2_m + σ^2_{pe} (Model 4)	3	-3637.75	0.00ns
FE + σ^2_a + σ^2_{pe} + $\sigma^2_{sire:site}$ (Model 5)	**3**	**-3635.17**	**5.16***

σ^2_a = additive variance; σ^2_m = maternal genetic variance; σ^2_{pe} = dam permanent environmental variance; $\sigma^2_{sire:site}$ = sire x site variance; #Critical values: 3.84 (P = 0.05); 6.64 (P = 0.01); * P < 0.05; ** P < 0.01; ns – not significant

The phenotypic variance components and variance ratios for additive genetic, dam genetic, dam PE and sire x site effects are presented in Table 2 for the respective models. The across flock heritability of FWEC ranged from 0.12 for Model 5 (the model of choice) to 0.16 for Model 1. Dam PE consistently contributed 0.03 to the phenotypic variation, while the sire x site variance amounted to somewhat more than 1% of the phenotypic variance. As FWEC was variable and heritable, genetic gains across flocks seems feasible although these gains may not necessarily be fast. The estimated heritability is within the ranges of 0.00 to 0.52 reported in the literature (Greeff *et al*. 1995; Safari and Fogarty 2003; Snyman 2007) and a fair reflection of previous heritability estimates within the flocks contributing data to this study (Cloete *et al*. 2007; Mpetile *et al*. 2015). The across-flock heritability of FWEC amounted to 0.16 for Australian meat sheep (Brown *et al*. 2016) and to 0.16 and 0.17 for Australian Merino yearlings and hoggets, respectively (Brown and Fogarty 2017). Maternal effects were not important in both latter studies. More comprehensive data on FWEC in the South African small stock industry is needed to allow the incorporation of this important input trait in the formal genetic evaluation scheme.

Table 2. The estimated phenotypic variance components and variance ratios for FWEC in across-flock analyses on Tygerhoek and Elsenburg Merinos for the random models fitted

Random model	σ^2_p	h^2	m^2	pe^2	sire.site
Model 1	0.817	0.16 ± 0.02	NA	NA	NA
Model 2	0.816	0.15 ± 0.02	0.02 ± 0.01	NA	NA
Model 3	0.815	0.14 ± 0.02	NA	0.03 ± 0.01	NA
Model 4	0.815	0.14 ± 0.02	0.00 ± 0.00	0.03 ± 0.01	NA
Model 5	0.815	0.12 ± 0.02	NA	0.03 ± 0.01	0.014 ± 0.006

σ^2_p – phenotypic variance; h^2 – heritability; m^2 – dam genetic effect; pe^2 – dam permanent environmental effect; sire.site – sire x site variance ratio; NA – not applicable

The dam PE estimate of 0.03 is somewhat lower than comparable estimates for FWEC of around 0.05 derived previously for the Tygerhoek flock (Cloete *et al*. 2007). It may well be that the accrual of additional pedigree information as well as sire x site effects partitioned animal variances away from dam PE in the present study. Corresponding values for PE effects sourced from the literature were variable from 0.02 to 0.16 (Safari and Fogarty 2003).

Although the observed variation for sire x site/season was significant in a Mediterranean climate, it contributed less than 2% to the overall phenotypic variation. Baker *et al*. (2004) did not find a significant G x E for FWEC in Red Masaai and Dorper sheep maintained under either sub-humid or

semi-arid conditions. Carrick and van der Werf (2007) reported highly variable genetic correlations between extreme quintiles for FWEC in Australian Sheep Genetics data. Some correlations involving FWEC were below 0.8, thus indicating the possibility of G x E. Since different methods were used, it is difficult to relate the present results to those of Carrick and van der Werf (2007). Both studies suggest the possibility of G x E for FWEC, although reranking among sires may be considered as small when the outcome of the present study is considered. The sire x site variance ratio in this study was on the lower end compared to previous estimates of between 2.2 and 2.5% of the variation attributed to sire x contemporary group for production traits in an across-flock analysis on South African Dohne Merinos (van Wyk *et al*. 2008). To our knowledge, there are no comparable studies exploring G x E for FWEC. An alternative approach that is worthy of exploration in future is the usage of random regression methods (Pollot and Greeff 2004; Hollema *et al*. 2018).

CONCLUSION

This study confirmed significant across-flock genetic variation in FWEC in South African sheep flocks. It therefore paves the way for further exploration of the genetic improvement of FWEC as an input trait in the local sheep industry. The derived heritability was not particularly high but backed by sufficient phenotypic variation to sustain genetic progress. Moreover, it is foreseen that further across-flock studies incorporating more flocks will provide more accurate estimations of other sources of variation, such as maternal effects and sire x flock effects.

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