

Exploring Genotype x Environment Interaction and Heritabilities for a Reproduction Trait in Merino Sheep Using Three Approaches

S. Dominik¹, J.E. Newton^{1,2}, B.J. Hayes³ and J.H.J. van der Werf^{2,4}

¹CSIRO Animal, Food and Health Sciences, Armidale, NSW, Australia ²University of New England, Armidale, NSW, Australia, ³Department of Primary Industries Victoria, Bundoora, VIC, Australia,

⁴Sheep CRC, Armidale, NSW, Australia.

ABSTRACT: Three approaches were used to detect genotype x environment (GxE) interaction and estimate heritabilities for “number of lambs born” (NLB) in Merino progeny of the Sheep CRC Information Nucleus Flock. Approaches included a univariate model, fitting site x sire interaction as a random effect and a bivariate model that treated NLB expressed at high and low pre-joining condition score as two genetically separate traits. The third approach was a random regression sire model that regressed NLB on mean deviation in pre-joining condition score at each experimental site from the overall mean of all sites. All approaches indicated that there was no significant GxE interaction for NLB. The consistently low heritabilities across all approaches also reflected that they did not differ in the partitioning of the variance components.

Keywords: Merino sheep; Genotype x environment interaction; Reproduction; Random regression

Introduction

Reproduction is one of the most important profit drivers in the Merino industry, but genetic progress is generally difficult to achieve due to low heritabilities for reproduction traits (Safari et al. (2005)). Low heritabilities could be due to several reasons, one reason being that traditionally measured traits, such as number of lambs born and weaned, might describe the complex processes underlying such traits insufficiently to capture the genetic variation. An alternative reason could be low accuracy at time of selection or that other sources of variance such as non-additive genetic effects or variation due to genotype x environment (GxE) interaction are important. Results of the few studies that have investigated GxE interaction for reproduction traits in sheep are variable and detected effects have undetermined effect on breeding programs (e.g. Fogarty et al. (2001), Notter et al. (2000 a,b)). Large data sets are required to explore the existence of GxE interactions comprehensively and possibly the definition of the environment as a physical entity, such as “flock”, might not be the most appropriate categorization to distinguish between environments in a relevant manner. The Australian Sheep CRC Information Nucleus Flock (INF) constitutes a large data set that could be used to investigate GxE interaction for reproduction traits in sheep, as common sires were used across a wide range of environments. Here we explore whether the definition of the environmental descriptor influences the ability to detect and extract variation associated with GxE

interaction and whether it affects the heritability for the trait of number of lambs born (NLB) in Merino sheep. We compare different definitions of ‘environment’ and different models to explore the interaction between environment and genotype for NLB.

Materials and Methods

Data. The data set originated from the Australian Sheep CRC INF and comprised records from eight sites (INF01-INF08) collected between 2007 and 2011 (van der Werf et al. (2010)). The reproduction trait analysed was “number of lambs born” (NLB) and we used records from purebred Merino ewes across two parities. The phenotypic data comprised a total of 4,592 records for NLB. A summary of the number of records is provided in Table 1. Out of 184 sires, 173 were used in two or more of the eight INF sites, with each sire having an average of 4-11 female reproduction records per site. The mean total number of records per sire across INF sites was 52 with a minimum number of 4 and a maximum of 212 records.

Table 1. Number of NLB records and number of ewes per INF site and environmental descriptor of pre-joining condition score (pj_cond) for each flock.

Environment	No of records	No of ewe records	pj_cond
IN01	1882	833	0.64 [§]
IN02	802	432	0.10 [§]
IN03	1030	473	0.31 [§]
IN04	876	506	-0.19 [§]
IN05	942	440	-0.22 [§]
IN06	868	379	-0.13 [§]
IN07	1104	613	-0.10 [§]
IN08	1938	916	-0.40 [§]
NLB _{low}	2355	1650	< 0.028 ^{&}
NLB _{high}	2114	1592	> 0.028 ^{&}

[§]mean site deviation from overall mean, [&]residual pj_cond

The analysis required an environmental descriptor that reflects a combination of climatic and local environmental conditions that affect reproduction. In one approach “site” was used as the environmental descriptor. However, INF site might not be a sufficient descriptor, because prevailing pasture conditions at each site might not reflect

feeding status appropriately as supplementary feeding occurred during feed shortages. Therefore, pre-joining condition score (pj_cond) of the ewe, recorded as a score ranging from 1 (low) to 5 (high), was also used as an environmental descriptor in a different approach. After adjusting the pj_cond phenotype for fixed effects and effect of sire, the data set was split based on residual pj_cond into ewes with residual pj_cond below (low pj_cond) or above (high pj_cond) the mean. Five percent of records immediately above and below the mean were discarded, to clearly distinguish the high and low pj_cond categories. A total of 3,242 ewes with records on both, NLB and pj_cond, were included in the analysis. Six hundred and sixty two ewes were represented in the high and low pj_cond environments due to multiple parities and 174 sires were represented across the two environments. On average each sire had 13 and 12 records in low and high pj_cond environments respectively, with number of records per sire ranging between 2 and 30.

Models. Three different models were used to investigate GxE interaction and estimate heritabilities for NLB. In Model 1, GxE interaction was defined as the variance associated with the sire x site interaction, fitting sire and sire x INF site as random effects in a univariate model for NLB. In Model 2, pj_cond of the ewe was defined as the “environment” and NLB expressed at high and low condition scores (NLB_{low} and NLB_{high}) were treated as two genetically different traits (Falconer (1952)). A bivariate animal model was then fitted to NLB_{low} and NLB_{high} and the genetic correlation (r_G) between the two traits indicates the existence of a GxE interaction. An estimated r_G significantly less than one would indicate the existence of a GxE interaction. Model 3 was a random regression sire model. It incorporated pj_cond in the definition of the environment by regressing NLB on the mean deviation in pj_cond score of individual INF sites from the overall mean of all sites (mean INF site deviation). A similar approach was used successfully in the context of GxE interaction on dairy data (Lillehammer et al. (2009)). The model included a random regression of sire on mean INF site deviation in pj_cond by fitting the interaction of sire and the first order Legendre polynomial on mean INF site deviation in pj_cond. A permanent environmental effect was fitted as a constant across parities and environments. Individual residual diagonal variance structures were specified for each INF flock.

All models included lambing year (2007 to 2011), birth-rearing type (three classes: born single/raised as single, born twin/raised as twin, born as twin/raised as single), INF site (Site 1 to 8), sire breed (Merino or Poll Merino) as fixed effects and pre-joining date (the date, when weights were recorded prior to mating) as covariate. (Co)variance components, heritabilities and correlations for Models 1 and 2 and the coefficients of covariance function (matrix K) for model 3 were estimated using ASReml (Gilmour et al (2002)). For the random regression model, the genetic (co)variances and heritabilities were estimated from matrix K as summarized by van der Werf et al. (1998). Correlations for all site combinations could be calculated as functions of the variances and co-variances from the matrix K.

Here only the correlations between IN08, the site with the lowest INF site deviation in pj_cond, with all sites ordered in increasing site deviation are shown.

Results and Discussion

In all models there was little evidence of GxE interaction for NLB. In the first model, the traditional approach was used to test potential GxE interactions by defining the environment as physical location, in this study “INF site”. The INF design allowed for good genetic linkage between sites through sires being used at two or more sites, which enabled fitting a sire x site variance component. The sire x site variance component only accounted for 4.5% of the phenotypic variation, but it accounted for 66% of the sum of variance due to genetic and interaction effects. This would indicate that a GxE interaction was present, but it accounted for little phenotypic variation.

In Model 2 NLB under low and high condition scores were treated as two separate traits and no conclusive evidence of a significant GxE interaction was revealed with an estimated genetic correlation of $r_G=0.66\pm 0.20$. The biological descriptor of condition score at time of joining was chosen, based on the assumption that it is an important driver of number of lambs born and reflects environmental conditions more appropriately than INF site. However, the high standard error indicated that more records are required to obtain a conclusive result with this approach.

In Model 3 a combination of the previous two descriptors of the environment were applied: the deviation of pj_cond at each INF site from the average pj_cond of all sites. The estimated genetic variance was low, as in Models 1 and 2, but a slight increase in genetic variance was observed with increasing mean site pj_cond (Figure 1). Residual variances differed along the trajectory with no clear trend, but clearly vary (Figure 2) The genetic correlations between NLB at low pj_cond deviation (IN08) and NLB expressed at all the other INF sites ranged from $r_G = 0.80-0.96$ with the majority being $r_G > 0.95$ (Figure 3). Again, this provides little evidence for a significant GxE interaction on NLB in Merino ewes in the INF.

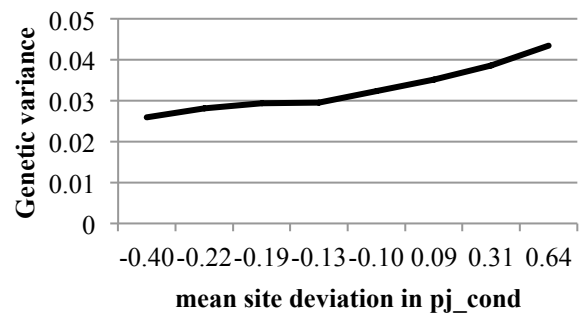


Figure 1: Genetic variances across the environmental trajectory (mean individual site deviation in pj_cond from all sites mean)

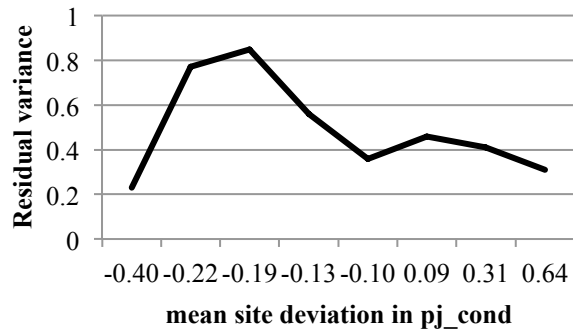


Figure 2: Residual variances across the environmental trajectory (mean individual site deviation in *pj_cond* from all sites mean)

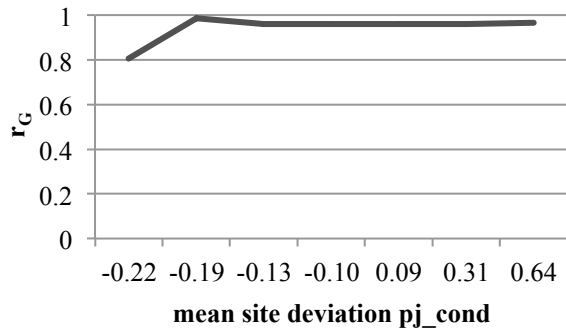


Figure 3: Genetic correlations of IN08 (lowest mean site deviation in *pj_cond* = -0.40) with other sites, ordered by increasing mean site deviation in *pj_cond*

Heritabilities were low for all models and the consistent results would indicate that variances were partitioned very similarly in the different analysis approaches, independent of the definition of the environmental descriptor (Table 2). The bivariate analysis yielded slightly higher heritabilities than the other approaches, due to higher genetic variance. The reason could be the environmental descriptor being another biological expression and even though it was adjusted for genetic effects of the sire, other effects, such as the genetic effect of the dam and effects from Mendelian sampling could still be unaccounted for and inflate the additive genetic variance. The difference in residual variances in the random regression approach (Figure 2) affects the heritabilities across the different environments somewhat, but because the genetic variances were generally low, heritabilities remained low.

Table 2 Heritabilities for NLB, NLB within high and low *pj_cond* (NLB_{low} and NLB_{high}) from Models 1 to 3

Model	Trait	h^2
1	NLB	0.09 ± 0.03
2	NLB _{low}	0.17 ± 0.04
2	NLB _{high}	0.14 ± 0.05
3	NLB	$0.02 - 0.12$

The random regression approach worked unexpectedly well on number of lambs born considering the moderate number of records, estimating the genetic variances in a probable range that agrees with reported estimates (Safari et al. (2005)). The advantage of the random regression analysis is that all co-variances can be estimated elegantly from a single analysis. The random regression approach relied on repeated daughter expressions of sires across the environmental descriptors, which was basically INF site. Sorting the INF site based on their deviation of *pj_cond* from the overall mean of all sites formed the trajectory for the repeat measures. Ideally an environmental descriptor would be based on repeated measures of condition score on a time trajectory, which then would allow the regression of NLB on condition score. This would remove the current confounding of the biological descriptor, such as *pj_cond* in this study with physical location, which was INF site in this study, and would also allow the estimation of residual covariances.

Conclusion

In this study different ways to characterize the environmental descriptor in GxE interaction models were compared. Besides the traditional approach of “sire x flock” we used condition score as a more biological meaningful ‘proxy’ for environment. Generally, no significant GxE interactions were found for number of lambs born in Australian Merino sheep and heritabilities were low. The random regression model was useful even for a trait of low heritability, such as number of lambs born and a moderate number of records. Compared to a bivariate model covariances can be estimated between all environments with one model using all data.

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