

SIRE BY ENVIRONMENT INTERACTION IN SHEEP MAY RE-RANK SIRES FOR SOME TRAITS

M.J. Carrick^{1,2} and J.H.J. van der Werf^{1,3}

¹Australian Sheep Industry Cooperative Research Centre

²Primary Industries Research Victoria, 475 Mickleham Rd, Attwood, VIC, 3049

³School of Rural Science & Agriculture, University of New England, Armidale, NSW, 2351

SUMMARY

Through analysis of field data from Sheep Genetics Australia, we estimated genetic correlations among breeding values in different environments, classified into quintiles by contemporary group averages for body weight (BWT), clean fleece weight (CFW) or weight of wool impurities (WIMP). A genetic correlation was considered to be low enough to be of concern if its upper 95% confidence limit was below 0.80, indicating a statistically significant genotype by environment interaction (GxE).

There appear to be significant GxE for body weight, eye muscle and fat depth in yearlings in all three environment classifiers and for hoggets classified on WIMP. The wool weights and to some extent also wool impurities also showed significant GxE in both yearling and hogget data. For the most part, wool quality traits were free of significant GxE interactions.

INTRODUCTION

Most breeders believe that important genotype by environment interactions (GxE) exist in wool-sheep, but there is little hard evidence. Most of this evidence comes from the work of Dunlop (1962, 1963) and Dunlop and Young (1966) who found Merino strain by location interactions for many traits but these were generally small. In addition, Woolaston (1987) suggested that Dunlop and Young's (1966) sire by location analysis fell well short of the minimum number of sires suggested by Robertson (1959). As a result, their estimates of the degree to which sire by environment interaction depressed genetic gain had little power. Woolaston (1987) reviewed the subject and examined these issues in more detail. In general the consensus in his review was that there appeared to be small but real strain by environment effects in sheep but that sire by environment effects were not yet known accurately.

There is much more information on sire by environment interactions in dairy cattle. Hayes *et al.* (2003) and Calus *et al.* (2005) showed that, whilst there were significant sire by environment interactions for milk traits, they were too low to be of concern (Robertson, 1959). Therefore, they found no reason to abandon the single Australian Breeding Value produced by the Australian Dairy Herd Improvement Scheme for each dairy trait.

It is clearly desirable for a national evaluation system to be kept to a manageable level of complexity, both for operational reasons and for effective extension purposes, so it is desirable to be able to assume no GxE. However, we need to test whether the assumption about the absence of GxE is correct or not. In view of the results by Dunlop (1962, 1963), Woolaston (1987) and of the dairy results of Hayes *et al.* (2003) and Calus *et al.* (2005), we set out to test our working hypothesis that breeding values were sufficiently constant across differing environments to require only a single estimate of sire breeding value for each trait in all environments.

MATERIALS AND METHODS

Data on wool quality, quantities, growth and carcase and faecal egg counts were obtained in 2005 from Sheep Genetics Australia but information was not available on location, climate, weather or pasture/feed supply. For this reason, the quality of the environment was estimated from contemporary group (CG) means for three separate classifying variables that could be thought of as reflecting differing parts of the environment: CG average body weight, clean fleece weight or weight of wool impurities. We used wool impurities rather than the more common yield measure to avoid part/whole correlations and difficulties in interpreting ratios, dividing the data into quintiles based on CG means and then estimating the genetic correlations among breeding values in different quintiles. This had the advantage of providing a sensible estimate of the interaction of sire by environment through the genetic correlation, among environment classifiers that did not exaggerate effects of extreme environments as can be the case in random regression.

The genetic correlation among quintiles can be estimated in different ways, one using an unstructured variance/covariance constraint, in which each correlation can reach any possible value and the other with an auto-regressive (AR) structure that assumes that only one auto-correlation is applicable. Between adjacent environments, this correlation is r . Between environments separated by two classes, it becomes r^2 , by three it becomes r^3 and between class 1 and 5 it becomes r^4 . The major advantage of this approach is that only one parameter is estimated from the whole set of data using few assumptions and avoiding the need to explain aberrant and poorly connected extremes. A possible disadvantage is a constrained correlation pattern masking non-linearities. For example, the AR model would not allow a correlation structure in which an extreme environment poorly correlated with the other 4 quintiles, but high correlations among the others. A genetic correlation was considered to be low enough to constitute a significant GxE if its upper 95% confidence limit was below 0.80 Robertson (1959).

Data were from the Sheep Genetics Australia database (December 2004) and contained a maximum of 259,600 records. Body weight (BWT), greasy and clean fleece weights (GFW, CFW) and fibre diameter (FD) measures were present at yearling or hogget age (up to 124,843 and 31,845 connected records respectively). Substantially fewer records contained eye muscle and fat depths (EMD, FAT), faecal egg counts (FEC) as well as coefficient of variation of fibre diameter (CVFD), fibre curvature (CURV), staple length and strength (SL, SS). Table 1 shows some examples of numbers of records and effective sire connectedness in the data set. The degree of connectedness is quite low in comparison with dairy data where AI is more widely practiced.

Table 1. Numbers of sires represented and the degree to which quintiles were connected in the yearling and hogget data sets. (examples)

Trait	Number of records	Total number of sires	Total connected sires	Effective connected sires (all quintiles)	Effective connected sires in quintiles (1, 5)
Y-BWT	101,559	4,376	2,464	1,611	94
Y-GFW	124,843	4,975	2,807	1,681	39
Y-CFW,FD	91,193	3,967	2,303	1,349	66
Y-FEC	37,126	1,729	677	453	13
H-GFW	31,845	1,371	554	389	90

Sheep 2

Connectedness was estimated by the method of Weeks and Williams (1964) which produces a connectedness coefficient (zero to one). When multiplied by the number of sires present in a pair of quintiles, an “effective number of sires” could be estimated for each quintile pair. This approximately represents the number of sires that would have been present if the data were balanced and fully connected. ASReml (Gilmour *et al.*, 2004) was used to model the correlation structures. Analyses were based on models fitting CG, sex and rearing type as fixed effects and sire x environment class as random effects. This is equivalent to a multivariate model but converges more easily.

Results

The three environment variables (contemporary group means) were all positively but weakly correlated. Correlations between CG means were 0.4 for BWT & WIMP, 0.67 for CFW & WIMP and 0.52 for BWT & CFW. The two approaches to estimating genetic correlations (US versus AR1) gave quite similar estimates where these were averages of four correlations (adjacent quintiles).

However between extremes, the single estimated correlation was more variable than averages. Importantly, even where the number of effectively connected sires was reasonably large in total (Table 1), the degree of effective connection between the extremes in this data set was much smaller. Discounting these poorly estimated genetic correlations at the extremes, the agreement between autoregressive and unstructured models is sufficiently close to tip the balance toward using the autoregressive model and consequently to use all the data to give a single genetic correlation estimate.

Table 2. Genetic correlation between top and bottom quintiles. Correlations significantly lower than 0.80 are shown in bold. These estimate a significant GxE.

Trait	Traits used to define quintiles based on CG means for yearling data			Traits used to define quintiles based on CG means for hogget data		
	Y-BWT	Y-CFW	Y-WIMP	H-BWT	H-CFW	H-WIMP
BWT	0.61	0.40	0.38	0.70	0.67	0.63
EMD	0.75	0.54	0.56	0.92	0.93	0.61
FAT	0.62	0.36	1.00	0.91	0.95	0.78
GFW	0.58	0.58	0.53	0.64	0.62	0.37
CFW	0.59	0.44	0.44	0.66	0.61	0.56
WIMP	0.84	0.68	0.62	0.80	0.48	0.57
FD	0.87	0.75	1.00	0.87	0.88	0.74
CVFD	0.83	0.89	0.69	0.83	0.88	0.90
CURV	0.96	0.89	0.88	1.00	1.00	1.00
SL	0.61	0.90	0.98	0.96	0.96	0.94
SS	0.92	0.94	0.80	0.87	0.79	0.85
FEC	0.30	0.04	0.95	0.86	0.95	0.56

Table 2 shows the worst case of genetic correlation between extreme quintiles which none-the-less represents 40% of the data. The body and carcass-related traits mostly show some GxE as do the wool quantity traits. However, there were generally few sire by environment class interactions among the wool quality traits. The yearling data appears to present relatively more GxE problems than

hogget measures and this may partly reflect differences in management practices such as lamb shearing. Faecal egg counts appeared to show fairly severe GxE.

DISCUSSION

Our working hypothesis, that EBVs are sufficiently stable as to not require adjustment for environmental influences, did not hold for some of the 12 traits studied. For wool weight and body weight, in all environment classifiers, the correlation among extremes for BWT, GFW and CFW were less than 0.8. Faecal egg counts showed evidence of GxE, but the estimates covered a very wide range. These estimates may be in error because location and Helminth type were unknown and some of the apparent GxE effect may be due to different species of worms or different lab personnel.

The other eight wool quality traits generally showed high genetic correlations across extreme environmental classes and therefore fit the working hypothesis. The wool traits affected by GxE in this study were confirmed by estimates in strain by environment studies by Dunlop (1962, 1963). Interactions for fleece weight and carcass traits are strong enough to require careful attention in the national genetic evaluation scheme. Results indicate that some care is needed in the development of the national evaluation because simulations of GxE suggest that loss of genetic gain can be substantial in some cases. When the Sheep Genetics Australia database has grown sufficiently to allow it, robust random regression analysis may be the method of choice both to evaluate the GxE and to implement EBV models which take it into account.

ACKNOWLEDGEMENTS

We are grateful to Dr Rob Woolaston and Dr Arthur Gilmour for their insights and generous assistance with the analyses. This study was funded by Meat and Livestock Australia, UNE and DPI Victoria through the Sheep CRC.

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