An investigation into possible genotype × environment interactions for weaning weight in South African Mutton Merino sheep

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Weaning weight records available for the South African Mutton Merino breed were utilised to investigate the possibility of a genotype by environment interaction in the breed. A direct heritability estimate of 0.308 ± 0.022 was obtained. Including flock-year-season × sire interaction (FYSXS) led to a direct heritability estimate of 0.017 ± 0.00 and a c^2_{FYSXS} estimate of 0.111 ± 0.00. Although flocks are genetically related by the use of rams from other flocks, very few of these rams are used in different flocks in the same year. Four flocks were hence selected where this did not seem a problem. This led to a direct heritability estimate of 0.125 ± 0.061 when interaction was included and a c^2_{FYSXS} estimate of 0.107 ± 0.019. The results indicate that a genotype × environment interaction in South African Mutton Merino exists. It is, however, impossible to quantify the effect of the interaction in a breed analysis because of the nature of the data structure. This is a general problem in sheep in South Africa, partly owing to the lack of use of AI across flocks.

Speenmassa-rekords van die Suid Afrikaanse Vleismerinoras is gebruik om 'n moontlike genotipe × omgewingsinteraksie te ondersoek. 'n Direkte oorerflikheid van 0.308 ± 0.022 is verkry. As kudde-jaar-seisoen × vaar interaksie (FYSXS) in die ontleding ingesluit word, daal die direkte oorerflikheid tot 0.017 ± 0.00 en 'n c^2_{FYSXS} beraming van 0.111 ± 0.00 word verkry. Omdat ramme van ander kuddes gebruik word, is die kuddes geneties gekoppel. Ramme word egter nie oor kuddes in dieselfde jaar gebruik nie. Vier kuddes waar die probleem nie bestaan nie, is vir 'n volgende ontleding gebruik. In die ontleding is 'n direkte oorerflikheid van 0.125 ± 0.061 en 'n c^2_{FYSXS} van 0.107 ± 0.019 verkry as interaksie ingesluit word. Hierdie resultate dui daarop dat 'n genotipe × omgewingsinteraksie wel in die Suid Afrikaanse Vliesmerinoras bestaan. Die datastruktuur maak dit egter onmoontlik om die effek van die interaksie in die ras te bepaal. Hierdie is 'n redelik algemene probleem in skaaprasse in Suid Afrika, deels omdat min KI oor kuddes heen gedoen word.

Keywords: Genotype × environment interaction, weaning weight, sheep, (co)variance components

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Introduction

Selection response in farm animals is often hampered by genotype × environment interaction. Van Tassel & Berger (1994) reported that even with relatively low levels of interaction, the biases in sire variance and heritability estimates were substantial when interaction was excluded from the model. They concluded that interaction should be included in the variance component model even if the data are only moderately unbalanced and herd by sire interaction is expected to be present at relatively low levels. Results obtained by Meyer (1987) in British Friesian-Holstein heifers and Neser *et al.* (1996) in Bonsmara cattle also suggest that bias existed if interaction was excluded from the analysis to estimate genetic parameters. Whereas the effect of herd-year-season × sire interaction in beef cattle is well documented (Bertrand *et al.*, 1985, 1987; Notter *et al.*, 1992; Brown *et al.*, 1993a, 1993b, Neser *et al.*, 1996), no literature evidence of the inclusion of flock-year-season by sire interaction (FYSxS) in sheep could be found.

The South African Mutton Merino is a wool bearing sheep breed, developed from the imported German Merino. It is found under a wide variety of environments that vary from highly intensive feeding to extensive conditions. It is therefore highly likely that a genotype × environment interaction could exist in the breed. The objective of this study was to examine a possible genotype × environment interaction in the South African Mutton Merino breed.

Material and methods

Data

Two different data sets were analysed. In the first, weaning weight records of 43 715 South African Mutton Merino lambs, the progeny of 970 sires in 87 flocks, were used. These were all the records available for the breed and were obtained from flocks from all over South Africa. A high number of rams exchange hands each year on the different ram sales. The result is that genetic links exist between the flocks. The number of sires with progeny across flocks in the same year is, however, limited. It is obvious that for meaningful results, sires should not be nested within FYS concatenations. It was possible to extract four flocks in which this did not seem to be a problem as a second data set. This consisted of 10 344 weaning weight records, the progeny of 172 sires.

Editing of the data entailed the following. All sires with less than five progeny and flock-year-season contemporary groups with only one sire were deleted. Only animals with full pedigree records were allowed in the analysis. This is normally not done when an animal model is used, but it was felt that when interactions are included this would be necessary.

Analysis

To assess the influence of non-genetic factors on weaning weight for inclusion in the model for both data sets, an analysis of variance was done using Harvey's LSMLMW programme (Harvey 1988). A significance level of $p < 0\ 01$ was used as criterium for inclusion.

Estimates of (co)variance components and heritabilities were obtained using the derivative-free Restricted Maximum Likelihood program (DFREML) developed by Meyer (1991, 1995). In the first analysis, using all the records, two correlated random factors, direct animal additive and maternal additive were included, while permanent maternal environment was included as an uncorrelated additional random factor as described by Meyer (1989). Meyer (1992), Meyer *et al.* (1993, 1994) and Neser *et al.* (1996) illustrated the importance of including permanent maternal environment in the analysis for weaning weight in beef cattle. Although Snyman *et al.* (1995) did not include permanent maternal environment in the analysis for weaning weight in Afrino sheep, she did stress the importance of this factor in birth weight. Flock-year-season, sex and birth status were included as fixed effects. Age at weaning and age of dam were fitted as linear and quadratic regressors. In the second analysis, again using all the records, flock-year-season by sire interaction was added as a second uncorrelated additional random factor. The factors included in the model in the first analysis were also included in the third analysis, while the fourth analysis shared the factors used in the second analysis. Both the third and fourth analyses were done using only the four selected flocks. The two models fitted in the four analyses were therefore:

$y = X\beta + Z_1a + Z_2m + Z_3c_1 + e$ (Model 1, used in 1st and 3rd analyses)

$y = X\beta + Z_1a + Z_2m + Z_3c_1 + Z_4c_2 + e$ (Model 2, used in 2nd and 4th analyses)

where y is an **nxl** vector of records, **X** is an **nxp** incidence matrix that relates data to the unknown vector of location parameters β. The vector β contained flock-year-season, sex and birth status as fixed effects while age of dam and age at weaning were included as linear and quadratic regressors. The incidence matrices $\mathbf{Z_1}$ and $\mathbf{Z_2}$ relate the unknown random vectors of direct breeding value **(a)** and maternal breeding value **(m)**, respectively, to **y**. The incidence matrices $\mathbf{Z_3}$ and $\mathbf{Z_4}$ relate the unknown additional random vectors of **FYSxS** interaction $(\mathbf{c_1})$ and permanent maternal environment $(\mathbf{c_2})$, also to **y**. The unknown vector **e** contains the random residuals owing to environmental effects peculiar to individual records.

Log likelihood tests were carried out to determine the most suitable model to analyse the data. A model was considered more suitable when a significant increase in the log likelihood occurred. Significance was assumed when minus two times the difference between the log likelihoods obtained from the different models used, was greater than the chi-square distribution with one degree of freedom. A significance level of $p < 0.01$ was used throughout.

Results and discussion

The heritability and (co)variance component estimates for the first two analyses are presented in Table 1.

With Model 1 (analysis 1) a direct heritability estimate of 0.31 was obtained. The results in the literature for mutton and dual purpose sheep breeds varies between 0.05 and 0.57 (Fogarty, 1995). Neser *et al.* (1995) obtained direct heritability estimates for weaning weight of 0.157 and 0.106 in two Dorper lines selected for weaning weight. These values correspond with the 0.128 obtained by Van Wyk *et al.* (1993) in Dormer sheep, but is lower than the 0.33 obtained by Snyman *et al.* (1995) in Afrino sheep. However, none of these authors did include flock-year-season × sire interaction in their models.

The inclusion of FYSxS interaction (Model 2, analysis 2) caused the direct heritability estimate to drop to almost zero (0.017). A c_I^2 estimate for FYSxS interaction of 0.11 was obtained. The maternal heritability also dropped to nearly half its original value, while the value obtained for permanent maternal environment remained constant. Although the log likelihoods (Table 2) indicate that FYSxS interaction should be included as an additional random factor, the fact that sires are largely nested within FYSs renders the analysis useless. Analysis 2 was merely undertaken to illustrate how poor data structure can lead to unrealistic estimations of, for instance, heritability, a key factor determining selection response. A heritability estimate approaching zero, implies that virtually no selection response is possible if selection is carried out over FYSs.

The results for the heritability and (co)variance component estimates from analysis 3 and 4 are presented in Table 3. The heritability and (co)variance component estimates obtained in analysis 3, using Model 1, closely represents the results obtained in the first analysis, which suggests that the four flocks chosen are a reasonably true reflection of the breed as a whole. When FYSxS interaction (Model 2) was included in the fourth analysis the direct additive heritability dropped to 0.125. This value corresponds to the results obtained by Van Wyk *et al.* (1993) in Dormer sheep and Neser *et al.* (1995) in Dorper sheep. Van Tassel & Berger (1994) also reported drastic increases in direct

Table 1 Heritability and (co)variance component estimates obtained in the first two analyses using the complete dataset

	Analysis 1 FYSxS excluded	Analysis2 FYSxS included
Direct heritability	0.308	0.017
SE	0.022	0.000
Maternal heritability	0.176	0.074
SE	0.021	0.002
Covariance as proportion of total	–0.158	-0.007
SE	0.019	0.000
Permanent maternal as additional random factor	0.085	0.085
SE	0.013	0.008
FYSxS as additional random factor		0.111
SE		0.000
Direct additive variance	7.456	0.418
Maternal additive variance	4.268	1.813
Covariance between animal effects	–3.189	0.166
Variance owing to permanent maternal	2.058	2.076
Variance owing to FYSxS		2.713
Error variance	14.273	17.205
Phenotypic variance	24.237	24.390
Correlation between direct and maternal effects	–0.677	0.191

Table 2 Log likelihood values[1] obtained under the first two analyses

Analysis 1	Analysis 2
721.20**	0.00

[1] As deviation from the most suitable model

** $p < 0.01$

heritability when interaction was removed from the model. It is interesting to note that the value obtained for FYSxS interaction was more or less the same as in the second analysis (0.111 vs 0. 107).

The FYSxS interaction in the fourth analysis is about 86% of the direct additive variance and about 11% of the phenotypic variance. This is higher than the values obtained by a number of authors for beef cattle (Bertrand *et al.*, 1985; Notter *et al.*, 1992; Neser *et al.*, 1996). According to Robertson (1959) the interaction is of biological importance when the genetic intra-class correlation between the performance of an animal in different environments is less than 0.8. The intra-class genetic correlation between performance of progeny of a sire in different environments can be written as $t = \delta^2_a/(\delta^2_a + 4\delta^2_a)$. In the fourth analysis a genetic correlation of 0.23 was obtained. This clearly indicates the existence of a genotype × environment interaction and would validify the inclusion of the FYSxS interaction as an additional random factor in the model. Meyer (1987)

Table 3 Heritability and (co)variance component estimates obtained in the third and fourth analyses using the second data-set

	Analysis 3 FYSxS excluded	Analysis 4 FYSxS included
Direct heritability	0.353	0.125
SE	0.035	0.061
Maternal heritability	0.171	0.087
SE	0.032	0.037
Covariance as proportion of total	–0.167	–0.038
SE	0.030	0.037
Permanent maternal as additional random factor	0.072	0.071
SE	0.018	0.024
FYSxS as additional random factor		0.107
SE		0.019
Direct additive variance	7.696	2.766
Maternal additive variance	3.735	1.920
Covariance between animal effects	–3.649	–0.846
Variance owing to permanent maternal	1.566	1.571
Variance owing to FYSxS		2.365
Error variance	12.460	14.358
Phenotypic variance	21.809	22.134
Correlation between direct and maternal effects	–0.681	–0.367

Table 4 Log likelihood values[1] obtained under the third and fourth analyses

Analysis 3	Analysis 4
146.70**	0.00

[1] As deviation from the most suitable model

** $p < 0.01$

reports that the exclusion of even a small genotype × environment interaction effect can lead to an overestimation of the predicted breeding values of animals. Van Tassel & Berger (1994) and Neser *et al.* (1996) concluded that the exclusion of a genotype × environment interaction factor could lead to bias in the estimation of genetic parameters in across-herd analyses.

Furthermore, the log likelihoods in Table 4 indicate that the inclusion of FYSxS interaction would be the most appropriate way to analyse the data. Unfortunately, because of sires nested within FYSs, the structure of the complete data set does not lend itself to be analysed in this way.

Conclusions

It is obvious that a genotype by environment interaction in the South African Mutton Merino breed exists. However, the structure of data on the breed prevents the quantification of the effect in the breed analysis. This is a general problem in sheep in South Africa, partly owing to the lack of the use of AI across flocks and years. To avoid unrealistic large differences between EBVs and too high expectations as far as response to selection is concerned, it is recommended that the heritability estimated in analysis 4 should be used initially. The introduction of a sire referring scheme to eliminate the problem of nested sires should be seriously considered.

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