Variance components and genetic parameters for body weight and fleece traits of Merino sheep in an arid environment

M.A. Snyman*, J.J. Olivier and W.J. Olivier

Grootfontein Agricultural Development Institute, Private Bag X529, Middelburg Cape, 5900 Republic of South Africa

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Data collected on the Carnarvon Merino flock over the period 1962 to 1983 were used for this study. Variance components resulting from direct additive genetic effects, maternal additive genetic effects, maternal permanent environmental effects, as well as the relationship between direct and maternal genetic effects for several body weight and fleece traits, were estimated by DFREML procedures. Traits analysed included 120-day weaning weight (WW), body weight (W6) and greasy-fleece weight (GFW6) at six months of age, as well as body weight (W18), clean fleece weight (CFW) and mean fibre diameter (MFD) at 18 months of age. By ignoring or including maternal genetic or environmental effects, four different models of analysis were fitted to determine the most suitable model for each trait. WW and GFW6 were significantly influenced by both maternal additive genetic and permanent environmental effects. For W6, W18 and CFW, the most suitable model included a direct as well as a maternal additive genetic effect, while only the direct additive genetic effect had a significant influence on MFD. Direct and maternal heritability estimates for the various traits were as follows: 0.14 and 0.11 for WW; 0.18 and 0.10 for W6; 0.20 and 0.06 for GFW6; 0.43 and 0.04 for W18; and 0.26 and 0.04 for CFW. A direct heritability of 0.60 was estimated for MFD. Standard errors for these estimates ranged from 0.01 to 0.04. Positive genetic correlations between direct and maternal genetic effects were estimated for WW (0.57), W6 (0.86) and W18 (1.00).

Data wat van 1962 tot 1983 op die Carnarvonse Merinokudde ingesamel is, is vir hierdie studie gebruik. Variansie-komponente vir direkte additiewe genetiese effekte, maternale additiewe genetiese effekte en maternale permanente omgewingseffekte vir verskeie liggaamsmassa en vageienskappe is deur middel van DFREML-prosedures beraam. Die volgende eienskappe is ontleed: 120-dae speenmassa (WW), liggaamsmassa (W6) en rouvagmassa (GFW6) op ses maande-ouderdom, sowel as liggaamsmassa (W18), skoonvagmassa (CFW) en veseldikte (MFD) op 18 maande-ouderdom. Om die mees geskikte model vir elke eienskap te bepaal, is vier verskillende modelle gepas deur maternale genetiese en omgewingseffekte te ignoreer of in te sluit. WW en GFW6 is betekenisvol deur maternale additiewe genetiese effekte sowel as maternale permanente omgewingseffekte beïnvloed. Die mees geskikte model in die geval van W6, W18 en CFW het direkte en maternale additief genetiese effekte ingesluit, terwyl slegs die direkte additief genetiese effek 'n invloed op MFD gehad het. Direkte en maternale oorerflikheidsberamings vir die verskillende eienskappe was soos volg: 0.14 en 0.11 vir WW; 0.18 en 0.10 vir W6; 0.20 en 0.06 vir GFW6; 0.43 en 0.04 vir W18; en 0.26 en 0.04 vir CFW. 'n Direkte oorerflikheid van 0.60 is vir MFD beraam. Standaardfoute vir hierdie beramings het gewissel van 0.01 tot 0.04. Positiewe genetiese korrelasies tussen die direkte en maternale genetiese effekte is vir WW (0.57), W6 (0.86) en W18 (1.00) beraam.

Keywords: Merino sheep, body weight, fleece traits, maternal effects, variance components, arid environment.

* Author to whom correspondence should be addressed

Introduction

A large percentage of the South African wool clip is produced from Merino sheep under extensive and, in some parts, arid environments. From the literature it is evident that most of the economically important traits in woolled sheep are moderately to highly heritable (Fogarty, 1995). This fact contributes to the general recommendation that selection on the individual's own performance will warrant substantial genetic gains. Recently it was shown that clean fleece weight at two-tooth age (age of final selection) is significantly influenced by a maternal additive genetic effect (Mortimer & Atkins, 1994; Hickson *et al.*, 1995). Olivier *et al.* (1994) also investigated the influence of additive genetic effects on two-tooth body weight, clean fleece weight and mean fibre diameter in the Grootfontein Merino stud. However, the environment in which the stud animals are run is not comparable to conditions under which most of the wool producing sheep in South Africa are kept. This is illustrated by the average 18 month body weight and clean fleece weight for the stud animals of 50.4 kg and 5.4 kg respectively. The influence of maternal effects on body weight and fleece traits of Merino sheep run in extensive environments in South Africa requires further study.

Genetic and environmental components of variance, and their ratios, form an integral part of any breeding plan. For genetic improvement of Merino sheep in South Africa, it is important that these components, especially under extensive environments, be known. The data collected on the experimental Merino flock ran at Carnarvon from 1962 until 1983 are one of the few data sets locally available for such genetic analysis. The objectives of this study were therefore, firstly, to determine the most suitable model of analysis for several body weight and fleece traits of Merino sheep in an arid environment and, secondly, to estimate variance components and genetic parameters for each of these traits.

Material and methods

Data

Data collected on the Carnarvon Merino flock over the period 1962 to 1983 were used for this study. A detailed description of the environment, animals, management and experimental procedures is given by Erasmus *et al.* (1990).

The Carnarvon Experimental Station is situated 18 km west of Carnarvon in the arid Karoo. The average annual rainfall during the experiment was 235 mm (SD = 108 mm). Temperatures varied between –9 °C and 39 °C, which is typical of a semi-desert climate.

Traits analysed were 120-day weaning weight (WW), body weight (W6) and greasy fleece weight (GFW6) at six months of age, as well as body weight (W18), clean fleece weight (CFW) and mean fibre diameter (MFD) at 18 months of age. CFW and MFD measurements were made as described by Erasmus *et al.* (1990).

The number of animals with data records, number of sires and dams with progeny in the data set, as well as the mean and coefficient of variation (CV) for each trait, are summarized in Table 1.

Variance components and genetic parameter estimation

Variance components were estimated using the DFREML program of Meyer (1989, 1991). Single trait animal models were fitted for all traits. All available pedigree information was used. By ignoring or including maternal genetic or environmental effects, four different models of analysis were fitted for each trait:

$$y = Xb + Z_1a + e \quad (1)$$

$$y = Xb + Z_1a + Z_2m + e \quad (3)$$

with $\mathrm{cov}(a,m) = 0$

$$y = Xb + Z_1a + Z_2m + e \quad (4)$$

with $\mathrm{cov}(a,m) = A\sigma_{am}$

$$y = Xb + Z_1a + Z_2m + Z_3c + e \quad (8)$$

with $\mathrm{cov}(a,m) = A\sigma_{am}$

where

y is a vector of observed traits of animals;

b, a, m and c are vectors of fixed effects, direct additive genetic effects, maternal additive genetic effects and maternal permanent environmental effects, respectively, and X, Z_1, Z_2 and Z_3 are the corresponding incidence matrices relating the effects to y;

e is the vector of residuals;

A is the numerator relationship matrix; and

σ_{am} is the covariance between direct additive genetic and maternal additive genetic effects.

It was assumed that:

$$V(a) = A\sigma^2_a;\ V(m) = A\sigma^2_m;\ V(c) = I\sigma^2_c;\ V(e) = I\sigma^2_e$$

where I is an identity matrix, σ^2_a, σ^2_m, σ^2_c and σ^2_e are the direct additive genetic variance, maternal additive genetic variance, maternal permanent environmental variance and residual variance respectively.

The following parameters were estimated: h^2_a (direct heritability); h^2_m (maternal heritability); c^2 (maternal permanent environmental variance as a proportion of phenotypic variance); c_{am} (covariance between direct and maternal additive genetic effects as a proportion of phenotypic variance); r_{Gam} (genetic correlation between direct and maternal additive genetic effects); and h^2_T (total heritability) (Willham, 1972).

The fixed part of the model for all traits included fixed effects for a year–sex subclass, a year–rearing status subclass and age of dam. For WW, W6 and GFW6, age of lamb (linear) was included as a covariate.

Log likelihood ratio tests were carried out among all four models to determine the most suitable model for each trait. Approximate sampling errors were calculated for each trait for the model which best described the respective data by fitting a quadratic function to the profile likelihood for each parameter involved (Meyer & Hill, 1992). Sampling errors for the genetic correlation between direct and maternal effects were calculated as described by Tosh & Kemp (1994).

Table 1 Description of the data set

Trait[a]	No. animals[b]	No. sires[c]	No. dams[c]	Mean	CV%
WW	8480	707	2710	20.75 kg	20.71
W6	6761	607	2240	21.59 kg	19.52
GFW6	7407	607	2240	1.18 kg	27.11
W18	6753	685	2560	35.18 kg	21.42
CFW	7371	685	2554	2.67 kg	25.84
MFD	7396	685	2557	19.52 μm	9.39

[a] WW = weaning weight
W6 = six month body weight
GFW6 = six month greasy fleece weight
W18 = 18 month body weight
CFW = 18 month clean fleece weight
MFD = 18 month fibre diameter

[b] with data records

[c] with progeny in the data

Results and discussion

It is evident from Table 1 that mean values for production traits in the Carnarvon Merino flock over the experimental period were less than the average production norms generally accepted for Merino sheep in South Africa. For example, the average body weight, CFW and MFD for Merino studs, tested at the SA Fleece Testing Centre from 1979 to 1988, were 48 kg, 4.25 kg and 21 μm respectively (Delport *et al.*, 1990).

Model specification

In Table 2, the log likelihood values obtained under the different models of analysis are summarized for each trait as deviations from the log likelihood value obtained under the most suitable model.

The most suitable model of analysis for WW and GFW6 was Model 8, which implies that both the maternal additive

Table 2 Log likelihood values[a] obtained for each trait under four different models of analysis

Trait	Model 1	Model 3	Model 4	Model 8
WW	–162.25**	–15.00**	–7.69**	0
W6	–90.37**	–17.36**	0	1.52
GFW6	–31.52**	–9.09**	–7.21**	0
W18	–47.66**	–27.95**	0	0
CFW	–5.33**	0	0.06	0.24
MFD	0	0.01	0.09	–0.09

[a] as deviation from the most suitable model

** $P < 0.01$

genetic effect, as well as the maternal permanent environmental effect had a significant influence on these two traits. The maternal permanent environmental effect in this study incorporated both similarities between twins and similarities between lambs born to the same ewe in different years. In this experiment, no ewes were culled on the basis of poor reproductive performance. Owing to the extremely poor environmental conditions in some years, young ewes had a very low body weight when they were mated at 18 months of age (average 32 kg). The strain of pregnancy and lactation, together with the fact that they themselves still had to grow, probably caused a 'setback' in these ewes. This 'setback' was subsequently carried over to the second and perhaps even the third parities, where the milk production of these ewes were also affected. Because WW and GFW6 are mainly produced while the lambs are still suckling, these two traits are influenced by any permanent environmental effect which affects the milk production of an ewe.

For W6 and W18, the most suitable model was Model 4, which included a direct as well as a maternal additive genetic effect, while allowing for a covariance between these two effects. A significant maternal additive genetic effect on body weight after weaning is also reported by Mortimer & Atkins (1994), Swan & Hickson (1994), Hickson *et al.* (1995), Mortimer & Atkins (1995), Snyman *et al.* (1995) and Vaez Torshizi *et al.* (1995). It would therefore be fair to assume that a carry-over maternal effect on body weight exists up to the age of 18 months in woolled sheep run under extensive conditions.

Model 3 provided the best fit of the data set in the case of CFW, while only the direct additive genetic effect (Model 1) had a significant influence on MFD. From these and other reported results (Mortimer & Atkins, 1994; Swan & Hickson, 1994; Hickson *et al.* (1995); Snyman *et al.*, 1995), it seems that CFW at 18 months of age was also subjected to a carry-over maternal genetic effect, but that MFD was not maternally influenced.

Genetic parameter estimates

Estimates of variance components and genetic parameters for the traits analysed, as estimated under the most suitable model for each trait, are presented in Tables 3 and 4 respectively.

The direct and maternal heritability estimates obtained for all traits analysed in this study fall within the ranges reported for Merino sheep worldwide (Erasmus *et al.*, 1990; Cloete *et al.*, 1992; Lewer *et al.*, 1994; Mortimer & Atkins, 1994; Olivier *et al.*, 1994; Swan & Hickson, 1994; Fogarty, 1995). It is also interesting to note that heritability estimates obtained in this study for Merino sheep in an arid environment are in accordance with those estimated for Merino sheep under intensive conditions at Tygerhoek (Cloete *et al.*, 1992) and Grootfontein (Olivier *et al.*, 1994).

Direct heritability estimates and variance components for body weight increased with age, while the corresponding maternal values declined. Direct genetic effects were, however, more important than maternal genetic effects for all traits analysed. Similar results were reported by Mortimer & Atkins (1995) for Merino sheep and by Snyman *et al.* (1995) for Afrino sheep at Carnarvon.

Table 3 Estimates of variance components[a] for WW, W6, GFW6, W18, CFW (kg^2) and MFD (μm^2)

Trait	σ^2_a	σ^2_m	σ_{am}	σ^2_c	σ^2_e	σ^2_p
WW	1.423	1.092	0.704	0.511	6.390	10.120
W6	1.877	0.995	1.180		6.396	10.448
GFW6	0.010	0.003	–0.002	0.003	0.038	0.052
W18	8.355	0.698	2.415		8.039	19.508
CFW	0.042	0.006			0.117	0.165
MFD	1.150				0.771	1.921

[a] σ^2_a = direct additive genetic variance
σ^2_m = maternal additive genetic variance
σ^2_c = maternal permanent environmental variance
σ_{am} = covariance between direct and maternal genetic effects
σ^2_e = residual variance
σ^2_p = phenotypic variance

Table 4 Estimates of genetic parameters[a] for WW, W6, GFW6, W18, CFW and MFD

Trait	h^2_a	h^2_m	c^2	c_{am}	r_{Gam}	h^2_T
WW	0.14	0.11	0.05	0.07	0.57	0.30
W6	0.18	0.10		0.11	0.86	0.40
GFW6	0.20	0.06	0.05	–0.03	–0.29	0.17
W18	0.43	0.04		0.12	1.00	0.63
CFW	0.26	0.04				0.27
MFD	0.60					0.60

SE range for h^2_a, h^2_m, c^2, c_{am} = 0.01 – 0.04; r_{Gam} = 0.10 – 0.31
[a] h^2_a = direct heritability
h^2_m = maternal heritability
c^2 = maternal permanent environmental variance as a proportion of phenotypic variance
c_{am} = covariance between direct and maternal additive genetic effects as a proportion of phenotypic variance
r_{Gam} = genetic correlation between direct and maternal additive genetic effects
h^2_T = total heritability

The covariance between direct and maternal genetic effects as a proportion of phenotypic variance (c_{am}) was 0.07, 0.11 and 0.12 for WW, W6 and W18 respectively. This resulted in high positive genetic correlations between direct and maternal effects (r_{Gam}) in these traits. Selection for increased body weight at any age could therefore be performed on single breeding values, based on total heritability estimates (h^2_T).

The negative r_{Gam} of –0.29 estimated for GFW6 in this study caused h^2_T (0.17) to be lower than h^2_a (0.20). Selection for fleece weight is however rarely done at such an early age and it would therefore have no practical implication.

Conclusion

From the results of this study it is evident that maternal effects contributed significantly to the genetic variance in almost all of the traits analysed, particularly in those traits measured at six months of age or younger. Even at two-tooth age, body weight and clean fleece weight were significantly influenced by a carry-over maternal genetic effect. Positive r_{Gam} estimated for body weight, together with the high total heritability estimates obtained for the economically important traits analysed in this study, confirmed the general recommendation that selection could be done on the animal's phenotype alone. Selection response can nevertheless be increased substantially if selection is based on BLUP of breeding values, as demonstrated by Olivier *et al.* (1995) in the Grootfontein Merino stud.

Heritability estimates for two-tooth body weight, clean fleece weight and mean fibre diameter obtained in this study, as well as other recently reported animal model heritability estimates, deviate from those used for the construction of a national selection index for Merino sheep (Poggenpoel, 1990). Direct genetic and phenotypic correlations among these traits need to be estimated under an animal model to determine the implications of possible differences between responses to the national selection index for Merino sheep and an index based on parameters derived from animal models.

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