

Estimation of genetic parameters and comparison of breeding values for body weight with different models in a South African Merino stud

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Abstract

Data collected on body weight from birth to 5 years of age in the Grootfontein Merino stud from 1968 to 2012 were analysed with univariate, multivariate and repeatability animal models. The estimated breeding values (EBVs) were compared to determine the most suitable statistical models for the estimation of EBVs. Measures of body weights included birth weight (BW), body weight at 42 days of age (W42), weaning weight (WW), body weight at 6 months (W6), 8 months (W8), 12 months (W12) and 15 months (W15) of age as well as adult weights recorded on the ewe flock from 2 to 5 years of age (AW2 to AW5). Univariate direct heritabilities were 0.20, 0.42, 0.16, 0.54, 0.43, 0.37, 0.51, 0.43, 0.40, 0.31 and 0.33 respectively. Multivariate direct heritabilities for WW, W12, W15 and AW3 were lower than those estimated with univariate models, namely 0.17, 0.22, 0.23 and 0.29 respectively. Direct heritability obtained with the repeatability model was 0.26. Maternal heritabilities for BW, W42, WW, W6, W8, and W15 were 0.11, 0.15, 0.04, 0.28, 0.18 and 0.08 respectively. Lower multivariate maternal heritabilities were obtained for WW (0.02) and W15 (0.01). The genetic correlation between direct and maternal effects was negative for all weights where it was included, ranging from -0.28 for BW to -0.95 for W6. High genetic correlations were estimated between weights at different ages with multivariate analyses. When animals were selected on EBVs estimated with multivariate models, 92% of the animals selected retained the same ranking. When using the Top 1% lists, 95% and 94% of the animals selected on either univariate (U) or multivariate (M) EBVs for W15 and WW respectively, would be identical. Selection based on univariate W15 EBVs, would possibly result in selection of different animals, due to lower rank correlations of W15U with WWU (0.67) and WWM (0.80) respectively. The moderate to high estimates of heritability for body weight demonstrated that there is still considerable additive genetic variation in body weight available. The present study indicated that the multivariate model was the most appropriate model for estimating breeding values for body weight at selection age in the Grootfontein Merino stud.

Keywords: Linear models, multivariate, repeatability, univariate, breeding values

Introduction

Growth is regarded as one of the most important traits for the selection of replacement animals in both wool and mutton sheep enterprises (Snyman & Cloete, 2008), as the growth rate and body weight of lambs at different ages determine the profitability of the enterprise (Mohammadi et al., 2013; Ngere et al., 2017). Body weight is positively correlated with many other traits of economic importance, such as reproduction (Safari et al., 2007b; Olivier & Cloete, 2011; Olivier, 2014), adaptability (Singh et al., 2016), wool production (Baneh et al., 2013; Olivier, 2014) and survival at birth (Baneh et al., 2013).

Over the past four decades, the focus of the South African Merino industry has been to increase body size, while ensuring that wool weight remains constant and fibre diameter is decreased (Olivier et al., 1995). Since 1996, the estimation of estimated breeding values (EBVs) has been done using a multiple trait model including body weight, clean fleece weight, fibre diameter and staple length. The current selection criteria of South African Merino sheep still mainly focus on growth and wool traits, but reproductive performance is also included (Herselman & Olivier, 2010; Van Graan et al., 2014). These selection strategies have resulted in positive genetic responses in the traits under selection (Olivier et al., 1995, Olivier, 2014).

A number of growth traits can be included as selection criteria. Birth weight is positively correlated with body weight at all other ages (Al-Shorepy, 2001), and is also associated with survival rate (Borg, 2007). Pre-weaning growth rate and weaning weight determines marketing age in lambs that are marketed at an early age (Boujenane & Diallo, 2017). Weaning weight is an important component of total weight of lamb weaned, which in turn determines ewe production efficiency. At least one measure of post weaning weight is routinely recorded in most sheep breeds and is usually related to the marketing weight of the breed. In South African Merino sheep, lambs could be marketed as early as 8 to 9 months of age under favourable conditions. The remaining animals that are not selected as replacement ewes or as castrated males for wool production are slaughtered at 15 to 18 months of age. Body weight at 12 to 16 months of age is included in the current selection index used for South African Merino sheep (Olivier et al., 2014).

Maternal effects affect early-expressed traits, such as pre-weaning and weaning weights. By including or omitting maternal effects, the accuracy of genetic parameters is influenced (Singh et al., 2016; Boujenane & Diallo, 2017). Ignoring maternal effects generally leads to an overestimation of heritability values, and unrealistic expectations regarding the rate of genetic progress that can be

achieved. It is important to apply the most appropriate model for the estimation of (co)variance components and genetic parameters for body weights. Restricted maximum likelihood models have been used extensively to estimate (co)variance components for body weight in sheep (Singh et al., 2016; Boujenane & Diallo, 2017; Kumar et al., 2017; Ngere et al., 2017). These models partition the phenotypic variance of a quantitative trait into additive genetic variance, environmental variance and other effects such as maternal, common environmental, or permanent environmental effects (Meyer, 1989). Arguably the simplest method of analysis of data with repeated measures is the repeatability model. In this model, each observation is treated as a repeated record of the same trait in the same individual. This model has been implemented in the past for traits such as milk yield in successive lactations in dairy cattle (Jamrozik et al., 1997; Interbull, 2000), and more recently for milk production in dairy sheep (Murphy *et al.*, 2017) and reproductive traits in Mehraban sheep (Yavarifard et al., 2015).

It is important that EBVs for performance traits should be estimated as accurately as possible. The aim of this study was to determine the most suitable statistical models for the estimation of breeding values for body weight in a South African Merino flock. Univariate, multivariate and repeatability animal models (Meyer & Hill, 1997; Gilmour et al., 2014) were compared to evaluate ranking of animals and accuracy of EBVs obtained with these different models.

Material and Methods

Data collected on the Grootfontein Merino stud were used for this study. Maintenance and selection procedures followed in the stud were described in detail by Olivier (1989, 1998) and Olivier et al. (1995). The dataset used in this study comprised body weight data recorded at different ages in this stud from 1968 to 2012. The total number of males and females for which birth weight was recorded, were 7794 and 8317 respectively (Table 1). The traits recorded were birth weight (BW), body weight at 42 days of age (W42), weaning weight (WW), body weight at 6 months (W6), 8 months (W8), 12 months (W12) and 15 months (W15) of age and adult weights recorded on the ewe flock from 2 to 5 years of age.

Table 1 Number of records, mean and coefficient of variation for body weights of ewes and rams

Trait	Number of records	Mean (kg)	Coefficient of variation (%)
Ewes			
Birth weight	8317	4.3	21.1
42-Day body weight	4077	16.5	24.5
Weaning weight	7602	26.1	21.4
6-Month body weight	641	32.5	20.0
8-Month body weight	848	36.5	15.6
12-Month body weight	1679	40.5	14.6
15-Month body weight	6441	42.4	16.2
2-Year body weight	2590	52.0	13.1
3-Year body weight	2313	55.4	12.6
4-Year body weight	1817	56.6	12.7
5-Year body weight	1437	56.6	13.4
Rams			
Birth weight	7794	4.5	20.3
42-Day body weight	3782	17.5	25.1
Weaning weight	7070	27.8	21.4
6-Month body weight	538	35.5	20.1
8-Month body weight	727	44.4	16.8
12-Month body weight	1515	53.7	23.7
15-Month body weight	4404	61.5	23.6

The fixed effects tested for significance were year-season of birth, sex, birth status, rearing status, age of the dam and their respective two-way interactions. Birth status was indicated as single (1), twin (2) or triplet (3) when born, while rearing status was indicated by the numerical indicating birth status followed by a numerical indicating whether the individual was reared as a single, twin or triplet. Age of the animal at recording was included as a covariate. The PROC GLM procedure of the SAS statistical package was used to determine which of these fixed effects had a significant influence on the different body weights (SAS, 2016).

The following model was applied for all body weights:

$$Y_{ijklmn} = \mu + ys_i + s_j + bs_k + rs_l + ad_m + (yss)_{ij} + b_1AL + e_{ijklmn}$$

Where

Y_{ijklmn} = trait of the n'th animal of the m'th age of dam of the l'th rearing status of the k'th birth status of the j'th sex of the i'th year-season of birth,

μ = overall mean,

ys_i = fixed effect of the i'th year-season of birth (1968 to 2012; depending on weight),

s_j = fixed effect of the j'th sex (ram, ewe),

bs_k = fixed effect of the k'th birth status (1 – single , 2 - twin, 3 - triplet; only for birth weight),

rs_l = fixed effect of the l'th rearing status (11, 21, 22, 31, 32, 33; for all except birth weight),

ad_m = fixed effect of the m'th age of dam (2 to 7 years),

$(yss)_{ij}$ = effect of the interaction between the i'th year-season of birth and the j'th sex,

b_1 = linear regression coefficient of the appropriate deviation from the mean of age of the lamb at recording (AL; except for birth weight),

e_{ijklmn} = random error with zero mean and variance $1\sigma^2_e$.

Uni- and multivariate linear animal models were fitted with the ASReml program (Gilmour et al., 2014). Direct additive and maternal additive genetic effects, with or without a covariance between them, and maternal permanent environmental effects were tested for all traits in six different combinations.

The six models were:

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

$$y = Xb + Z_1a + Z_3mpe + e \quad (2)$$

$$y = Xb + Z_1a + Z_2m + e; \text{ with } cov(a,m) = 0 \quad (3)$$

$$y = Xb + Z_1a + Z_2m + e; \text{ with } cov(a,m) = A\sigma_{am} \quad (4)$$

$$y = Xb + Z_1a + Z_2m + Z_3mpe + e; \text{ with } cov(a,m) = 0 \quad (5)$$

$$y = Xb + Z_1a + Z_2m + Z_3mpe + e; \text{ with } cov(a,m) = A\sigma_{am} \quad (6)$$

where y was a vector of observed traits of animals; b , a , m and mpe were vectors of fixed effects, direct additive genetic effects, maternal additive genetic effects and maternal permanent

environmental effects respectively; X , Z_1 , Z_2 and Z_3 were incidence matrices respectively relating fixed effects, direct additive genetic effects, maternal additive genetic effects and maternal permanent environmental effects to y ; e was the vector of residuals; A was a numerator relationship matrix, and σ_{am} was the covariance between direct additive genetic and maternal additive genetic effects. It was assumed that $V(a) = A\sigma_a^2$; $V(m) = A\sigma_m^2$; $V(mpe) = I\sigma_{mpe}^2$; $V(e) = I\sigma_e^2$, where I was an identity matrix, σ_a^2 , σ_m^2 , σ_{mpe}^2 and σ_e^2 were the direct additive genetic variance, maternal additive genetic variance, maternal permanent environmental variance and environmental variance respectively. All components, with the phenotypic variance (σ_p^2), being the sum of σ_a^2 , σ_m^2 , σ_{am} , σ_{mpe}^2 , and σ_e^2 , were derived at convergence.

Depending on the model, variance ratios were computed as direct heritability ($h_a^2 = \sigma_a^2/\sigma_p^2$), maternal heritability ($h_m^2 = \sigma_m^2/\sigma_p^2$) and the direct-maternal covariance as proportion of phenotypic variance ($C_{am} = \sigma_{am}/\sigma_p^2$), with a corresponding estimate of the direct-maternal correlation [$r_{am} = C_{am} / \sqrt{(\sigma_a^2 \times \sigma_m^2)}$]. Similarly, the maternal environmental variance ratio was estimated by the permanent maternal environmental variance as a proportion of σ_p^2 ($c_{mpe}^2 = \sigma_{mpe}^2/\sigma_p^2$).

Different methods were used to determine the most suitable model for analysis. The likelihood ratio statistic [$\text{Log}L$; $\log\sigma = L(b_2) - L(b_1)$, where $L(b)$ is the log likelihood function evaluated at the maximum likelihood estimator (b)], was one method used (Morrell, 1998). The statistic $-2(\log L_2 - \log L_1)$ has a χ^2 distribution with degrees of freedom equal to the difference between the number of parameters for the two models being compared. An effect was considered to have a significant influence when its inclusion caused a significant increase in log likelihood, compared to the model in which it was ignored. For the purpose of this study, a significance level of $P < 0.05$ was applied throughout. Meyer (2004) stated that this test favours the model with the most parameters.

Akaike information criterion (AIC; Akaike, 1974), is $AIC = -2 \log L + 2k$, where L is the likelihood and k is the number of parameters. The model with the smallest AIC is preferred. Schwarz Bayesian information criterion (BIC, Schwarz, 1978), is $BIC = -2 \log L + k \log n$, where L is the likelihood, k is the number of parameters and n is the number of observations (sample size). The model with the lower value of BIC is preferred.

Subsequently, a multivariate analysis, including weaning weight, 12-month body weight, 15-month body weight and adult ewe body weight at three years of age, was done. The most suitable model for each trait, as determined under univariate analyses, was fitted for each weight.

The estimation of the genetic parameters with repeatability models was also done with the ASReml program (Gilmour et al., 2014). Fixed effects for year-season of birth, sex, rearing status and age of the dam were included in the models. Direct additive and maternal additive genetic effects, with or without a covariance between them, animal permanent environmental effects and maternal permanent environmental effects were tested for all body weights in different combinations to yield six possible models. Two sets of these models were run. In the first, splines were fitted to separate ages 1, 2, 4, 6, 8, 12, 15, 20, 32, 44, 56 and 68 months, while the second set of six models were run without the splines. The six models were:

$$y = Xb + Z_1a + W_1anim + e \quad (1)$$

$$y = Xb + Z_1a + W_1anim + W_2mpe + e \quad (2)$$

$$y = Xb + Z_1a + Z_2m + W_1anim + e; \text{ with } \text{cov}(a,m) = 0 \quad (3)$$

$$y = Xb + Z_1a + Z_2m + W_1anim + e; \text{ with } \text{cov}(a,m) = A\sigma_{am} \quad (4)$$

$$y = Xb + Z_1a + Z_2m + W_1anim + W_2mpe + e; \text{ with } \text{cov}(a,m) = 0 \quad (5)$$

$$y = Xb + Z_1a + Z_2m + W_1anim + W_2mpe + e; \text{ with } \text{cov}(a,m) = A\sigma_{am} \quad (6)$$

where y was a vector of observed traits of animals; b , a , m , $anim$ and mpe were vectors of fixed effects, direct additive genetic effects, maternal additive genetic effects, animal permanent environmental effects and maternal permanent environmental effects respectively; X , Z_1 , Z_2 , W_1 and W_2 were incidence matrices respectively relating fixed effects, direct additive genetic effects, maternal additive genetic effects, animal permanent environmental effects and maternal permanent environmental effects to y ; e was the vector of residuals; A was a numerator relationship matrix, and σ_{am} was the covariance between direct additive genetic and maternal additive genetic effects. It was assumed that $V(a) = A\sigma_a^2$; $V(m) = A\sigma_m^2$; $V(anim) = I\sigma_{anim}^2$; $V(mpe) = I\sigma_{mpe}^2$; $V(e) = I\sigma_e^2$, where I was an identity matrix, σ_a^2 , σ_m^2 , σ_{anim}^2 , σ_{mpe}^2 and σ_e^2 were the direct additive genetic variance, maternal additive genetic variance, animal permanent environmental variance, maternal permanent environmental variance and environmental variance respectively. All components, with the phenotypic variance (σ_p^2), were derived at convergence. The same statistics, namely, LogL, AIC and BIC were used to determine the most suitable model for analyses.

EBVs were estimated for WW and W15, which are used for selection in the South African Small stock improvement scheme (NSIS). WW is used as selection criteria for reproduction, while W15 is the body weight included in the selection index at selection age as a measure of growth potential. AW3 was included as an indication of mature ewe body weight. As genetic correlations among the pre-weaning body weights, among the post-weaning weights and among the adult body weights are high and positive, the evaluation of EBVs for WW, W15 and ABW3 could be taken as representative of the different growth stages. The breeding values obtained for weaning weight, weight at 15 months and 3-year body weight estimated using the most suitable univariate models, multivariate model and repeatability model, were compared. Estimated breeding values and accuracies of body weights of individual animals were obtained as back solutions with the ASReml program (Gilmour et al., 2014). Accuracy of EBVs were calculated as $\sqrt{1 - [(predicted\ error\ variance\ reported\ with\ each\ BLUP\ value)^2 / additive\ genetic\ variance\ of\ the\ specific\ trait]}$.

A dataset comprising EBVs for all animals with a 15-month body weight record was compiled. This implies that animals that had died before the age of 15 months were removed from the data set used for the following analyses. The Spearman rank correlation under the PROC CORR-procedure of SAS (SAS, 2016) was used to estimate the correlations between the ranks of these estimated breeding values for the different models. Furthermore, lists were compiled of the Top 10% and Top 1% of the animals having the highest EBVs for weaning weight, weight at 15 months and 3-year body weight, estimated with the different procedures. The number and percentage of animals common to the top lists were evaluated among the procedures.

Results

The number of records, means and coefficients of variation (CV) of the different body weights for the ewes and rams are presented in Table 1. The total number of records available for analysis ranged from 538 (rams) and 641 (ewes) for 6-month body weight to 7794 (rams) and 8317 (ewes) for birth weight, respectively. Relatively fewer records were available for 6-, 8- and 12-month body weights as body weights at these ages were not routinely recorded over the study period. The number of records decreased with age of ewes, due to culling and mortality.

The results of the non-genetic effects tested for significance for each trait, are summarised in Table 2. Year-season of birth had a significant ($P < 0.001$) effect on all the traits studied, while sex and birth status had a significant ($P < 0.001$) effect on all the traits for which these effects were included.

Table 2 Significance level of the different non-genetic effects tested for the respective traits

Trait	Year/season of birth	Sex	Birth status	Rearing status	Age of dam	Year/season of birth * Sex	Age of animal
Birth weight	*	*	*	-	ns	ns	-
42-Day body weight	*	*	-	*	ns	ns	*
Weaning weight	*	*	-	*	*	*	*
6-Month body weight	*	*	-	*	*	ns	*
8-Month body weight	*	*	-	*	*	*	*
12-Month body weight	*	*	-	*	ns	-	*
15-Month body weight	*	*	-	*	*	*	*
2-Year body weight	*	-	-	ns	ns	ns	ns
3-Year body weight	*	-	-	ns	ns	ns	ns
4-Year body weight	*	-	-	ns	ns	ns	ns
5-Year body weight	*	-	-	ns	ns	ns	ns

* $P < 0.001$; ns = not significant, - = not included

The Log L information criteria given in Table 3 indicate the most suitable model for each trait and were supported by the AIC and BIC criteria (data not shown). Model 6 which included all random effects, as well as the covariance between additive and maternal genetic effects was the most suitable model for BW, W42, W6 and W8. Model 5, including all the random effects, but excluding the covariance between the additive and maternal genetic effects was the most suitable for WW. The most suitable model (Model 2) for W12 included only the additive genetic and maternal permanent environmental effects, while Model 4, including additive and maternal genetic effects, as well as the covariance between these effects, was the most suitable model for W15. For all the adult body weights, either maternal genetic or maternal permanent environmental effects were included in addition to the additive genetic effect. For AW3 and AW5, Model 2 and Model 3 yielded the same results in terms of both

information criteria and genetic parameters. Model 3 was chosen for further analyses and discussion of variances and genetic parameters.

Table 3 LogL values as a deviation from the most suitable model (Most suitable model highlighted)

Trait	M1	M2	M3	M4	M5	M6
BW	833.96	57.28	97.26	87.34	7.24	0
W42	338.96	50.42	99.2	47.36	45.78	0
WW	973.50	26.34	56.92	55.48	2.20	0
W6	14.60	7.26	13.84	9.46	7.26	0
W8	38.30	13.58	31.64	20.84	13.58	0
W12	6.78	0	4.64	3.34	0	0.46
W15	52.20	44.68	34.04	1.30	34.04	0
AW2	270.50	0	3.28	3.08	0	1.56
AW3	179.08	0	0	1.32	0	1.06
AW4	169.52	1.12	0.58	0	0.58	0
AW5	133.26	0.02	0.02	0	0.02	0
AW6	53.36	3.16	2.84	0	2.84	0

BW = birth weight; W42 = body weight at 42 days of age; WW = Weaning weight; W6 = body weight at 6 months of age; W8 = body weight at 8 months of age; W12 = body weight at 12 months of age; W15 = body weight at 15 months of age; AW2 = adult body weight at two years; AW3 = adult body weight at three years; AW4 = adult body weight at four years; AW5 = adult body weight at five years; AW6 = adult body weight at six years

Table 4 summarises the (co)variance ratios for the various body weights obtained using the most suitable univariate model for each trait. Phenotypic variance increased with age until W15, after which it tended to plateau, while environmental variance kept increasing with an increase in age. No definite trend in direct genetic variance, maternal genetic variance or the maternal permanent environmental variance could be discerned with an increase in age.

Table 4 (Co)variance components for the various body weights estimated with the most suitable univariate model for each weight

Trait	Model	σ^2_p	σ^2_a	σ^2_m	σ^2_{mpe}	σ_{am}	σ^2_e
BW	M6	0.570	0.117	0.065	0.071	-0.025	0.343
W42	M6	12.003	5.084	1.748	1.272	-2.407	6.306
WW	M5	19.262	3.088	0.943	1.661		13.570
W6	M6	26.335	14.280	7.565	3.829	-9.860	10.521
W8	M6	28.980	12.571	5.131	5.982	-7.436	12.732
W12	M2	29.608	10.837		1.375		17.396
W15	M4	34.264	17.558	2.693		-3.540	17.553
AW2	M2	28.466	12.357		1.476		14.633
AW3	M3	31.525	12.467	0.000			19.059
AW4	M3	34.315	10.569	0.736			23.010
AW5	M3	34.223	11.397	0.000			22.826

σ^2_p = Phenotypic variance; σ^2_a = direct additive variance; σ^2_m = maternal additive variance; σ^2_{mpe} = maternal permanent environmental variance; σ_{am} = genetic covariance between the animal effects; σ^2_e = environmental variance; BW = birth weight; W42 = body weight at 42 days of age; WW = weaning weight; W6 = body weight at 6 months of age; W8 = body weight at 8 months of age; W12 = body weight at 12 months of age; W15 = body weight at 15 months of age; AW2 = adult body weight at two years; AW3 = adult body weight at three years; AW4 = adult body weight at four years; AW5 = adult body weight at five years

Table 5 presents the genetic parameters for the different body weights obtained using the most suitable model for each trait. Direct heritability estimates were medium to high, ranging from 0.16 (WW) to 0.54 (W6). No definite trend was observed for direct heritability with increasing age. Maternal heritability values were lower than the corresponding direct heritabilities for all body weights, with the highest value of 0.28 reported for W6. The c^2_{mpe} estimates ranged from 0.05 for W12 and AW2 to 0.21 for W8. The genetic correlation between direct and maternal effects was negative for all weights where it was included. The relatively high standard errors of the parameters estimated for 6- and 8-month body weight could most probably be ascribed to the fewer records available for these traits, namely less than 1200 for W6 and less than 1600 for W8.

Table 5 Direct additive heritability (h^2_a), maternal heritability (h^2_m), maternal permanent environmental effect (c^2_{mpe}) and the genetic correlation between the animal effects (r_{am}) for the various body weights (\pm s.e.) estimated with univariate models

Trait	Model	h^2_a	h^2_m	c^2_{mpe}	r_{am}
BW	M6	0.20 \pm 0.03	0.11 \pm 0.02	0.12 \pm 0.01	-0.28 \pm 0.09
W42	M6	0.42 \pm 0.06	0.15 \pm 0.03	0.10 \pm 0.02	-0.81 \pm 0.05
WW	M5	0.16 \pm 0.02	0.04 \pm 0.01	0.09 \pm 0.01	
W6	M6	0.54 \pm 0.15	0.28 \pm 0.17	0.15 \pm 0.05	-0.95 \pm 0.14
W8	M6	0.43 \pm 0.11	0.18 \pm 0.08	0.21 \pm 0.04	-0.93 \pm 0.10
W12	M2	0.37 \pm 0.05		0.05 \pm 0.02	
W15	M4	0.51 \pm 0.04	0.08 \pm 0.02		-0.51 \pm 0.06
AW2	M2	0.43 \pm 0.05		0.05 \pm 0.03	
AW3	M3	0.40 \pm 0.05	0.00 \pm 0.00		
AW4	M3	0.31 \pm 0.06	0.02 \pm 0.03		
AW5	M3	0.33 \pm 0.06	0.00 \pm 0.00		

h^2_a = direct heritability; h^2_m = maternal heritability; c^2_{mpe} = maternal permanent environmental effect; r_{am} = genetic correlation between direct and maternal effects; BW = birth weight; W42 = body weight at 42 days of age; WW = Weaning weight; W6 = body weight at 6 months of age; W8 = body weight at 8 months of age; W12 = body weight at 12 months of age; W15 = body weight at 15 months of age; AW2 = adult body weight at two years; AW3 = adult body weight at three years; AW4 = adult body weight at four years; AW5 = adult body weight at five years

The (co)variance components, correlations and heritabilities obtained with multivariate analyses of WW, W12, W15 and AW3 are summarised in Table 6. Direct heritability increased from 0.17 \pm 0.02 for WW to 0.29 \pm 0.04 for AW3. Phenotypic correlations among the traits ranged from low (0.36 \pm 0.02 between WW and AW3) to high (0.73 \pm 0.01 between W12 and W15). Genetic correlations were generally high and ranged from 0.69 \pm 0.05 between W12 and W15 to 0.85 \pm 0.05 between WW and W12.

Table 6 Covariance components, correlations and heritabilities among WW, W12, W15 and AW3 obtained with multivariate analyses

Trait	Parameter	WW	W12	W15	AW3
WW	σ_{p1p2}	22.387	16.932	14.950	12.030
W12	σ_{p1p2}		58.723	46.328	33.808
W15	σ_{p1p2}			67.799	39.852
AW3	σ_{p1p2}				51.143
WW	σ_{a1a2}	3.851	5.980	6.477	5.757
W12	σ_{a1a2}		12.792	9.828	10.032
W15	σ_{a1a2}			15.967	11.644
AW3	σ_{a1a2}				14.852
WW	σ_m^2	0.411			
W15	σ_m^2			0.419	
WW	σ_{mpe}^2	1.861			
W12	σ_{mpe}^2		0.000		
WW	σ_{e1e2}	16.234	10.952	8.473	6.273
W12	σ_{e1e2}		45.931	36.500	23.775
W15	σ_{e1e2}			51.413	28.208
AW3	σ_{e1e2}				36.291
WW	r_{p1p2}	-	0.47 ± 0.01	0.38 ± 0.01	0.36 ± 0.02
W12	r_{p1p2}		-	0.73 ± 0.01	0.62 ± 0.02
W15	r_{p1p2}			-	0.68 ± 0.01
AW3	r_{p1p2}				-
WW	r_{g1g2}	-	0.85 ± 0.05	0.83 ± 0.04	0.76 ± 0.06
W12	r_{g1g2}		-	0.69 ± 0.05	0.73 ± 0.07
W15	r_{g1g2}			-	0.76 ± 0.05
AW3	r_{g1g2}				-
WW	h_a^2	0.17 ± 0.02			
W12	h_a^2		0.22 ± 0.03		
W15	h_a^2			0.23 ± 0.02	
AW3	h_a^2				0.29 ± 0.04
WW	h_m^2	0.02 ± 0.01			
W15	h_m^2			0.01 ± 0.0	

Trait	Parameter	WW	W12	W15	AW3
WW	c^2_{mpe}	0.08 ± 0.01			
W12	c^2_{mpe}		0.00 ± 0.00		

σ_{p1p2} = Phenotypic covariance; σ_{a1a2} = direct additive covariance; σ^2_m = maternal additive variance; σ^2_{mpe} = maternal permanent environmental variance; σ_{e1e2} = environmental covariance; r_{p1p2} = phenotypic correlation; r_{g1g2} = genetic correlation; h^2_a = direct heritability; h^2_m = maternal heritability; c^2_{mpe} = maternal permanent environmental effect; WW = weaning weight; W12 = body weight at 12 months of age; W15 = body weight at 15 months of age; AW3 = adult body weight at three years

According to the Log L, AIC and BIC values, Model 3 without splines was identified as the most appropriate model for estimation of genetic parameters for body weight using a repeatability model. Variance components and genetic parameters estimated with the respective models are presented in Table 7.

Table 7 Variance component and genetic parameter estimates for body weight estimated with the most suitable repeatability model

Parameter	Model 3
σ^2_p	30.056
σ^2_a	7.918
σ^2_m	2.341
σ^2_{anim}	3.332
σ^2_e	16.466
h^2_a	0.26 ± 0.06
h^2_m	0.08 ± 0.03
c^2_{anim}	0.11 ± 0.05
t	0.37 ± 0.04

σ^2_p = Phenotypic variance; σ^2_a = direct additive variance; σ^2_m = maternal additive variance; σ^2_{anim} = animal permanent environmental variance; σ^2_e = environmental variance; h^2_a = direct additive heritability; h^2_m = maternal heritability; c^2_{anim} = animal permanent environmental effect; t = repeatability

Higher direct additive heritability values were obtained with the univariate models (U) for W12 (0.37 vs. 0.22), W15 (0.51 vs. 0.23) and AW3 (0.40 vs. 0.29) compared to the multivariate (M) model. The maternal heritability values followed the same trend, with higher values estimated for both WW and

W15 using the univariate model. As the repeatability model (REP) yielded one heritability for body weight overall, it is not possible to compare repeatability model values with specific uni- or multivariate values for each of the different body weights.

Spearman rank correlations between EBVs obtained with univariate, multivariate and repeatability animal models for WW, W15 and AW3 were estimated for all animals in the pedigree file with a 15-month body weight data record (Table 8). High correlations were obtained between the EBV rankings of WWU, W15U, WWM and W15M, while much lower correlations were observed between univariate estimates at 3 years of age (AW3U) and the other traits. These correlations increased when AW3 was included in the multivariate analyses. High correlations were estimated among EBVs of the traits included in the multivariate model, while low correlations were obtained between the rankings of the repeatability model EBVs and all other EBVs.

Table 8 Spearman rank correlations between EBVs obtained with univariate, multivariate and repeatability animal models for WW, W15 and AW3 using all animals with 15-month body weight data

Trait	WWU	W15U	AW3U	WWM	W15M	AW3M	REP
WWU	-	0.67	0.26	0.85	0.70	0.70	0.30
W15U		-	0.23	0.80	0.88	0.77	0.27
AW3U			-	0.32	0.25	0.52	0.12
WWM				-	0.92	0.92	0.26
W15M					-	0.91	0.23
AW3M						-	0.22

WWU = Weaning weight univariate; W15U = 15-month body weight univariate; AW3U = 3-year adult body weight univariate; WWM = Weaning weight multivariate; W15M = 15-month body weight multivariate; AW3M = 3-year adult body weight multivariate; REP = Repeatability model; All correlations significant ($P < 0.001$)

The number and proportion of common animals in the Top 10% and Top 1% lists are presented in Table 9 for EBVs estimated with the different models for weaning weight, 15-month body weight and 3-year body weight. The highest percentage common animals for the Top 10% lists was between the W15U and W15M lists which had 64.36% animals in both lists. The same applied for the Top 1% lists, where 95.33% common animals were present in the W15U and W15M lists. The lists involving the repeatability model EBVs had the least number of common animals. For all traits, the Top 1% lists had a higher percentage common animal than the Top 10% lists.

Table 9 The number and proportion of common animals in the Top 10% and Top 1% lists when animals with a 15-month body weight data record were included

Models	Top 10% list		Top 1% list	
	(n = 1069)		(n = 107)	
	Number	%	Number	%
WWU vs WWM	658	61.55	101	94.39
WWU vs REP	385	36.01	53	49.53
WWM vs REP	391	36.58	44	41.12
W15U vs W15M	688	64.36	102	95.33
W15U vs REP	362	33.86	48	44.86
W15M vs REP	376	35.17	37	34.58
AW3U vs AW3M	468	43.78	93	86.92
AW3U vs REP	174	16.28	22	20.56
AW3M vs REP	333	31.15	27	25.23

WWU = Weaning weight univariate; W15U = 15-month body weight univariate; AW3U = 3-year adult body weight univariate; WWM = Weaning weight multivariate; W15M = 15-month body weight multivariate; AW3M = 3-year adult body weight multivariate; REP = Repeatability model

Table 10 The mean, minimum and maximum of the accuracies (%) of the EBVs of all animals in the pedigree for WW, W15 and AW3 obtained with univariate, multivariate and repeatability animal models

Trait	Mean	Minimum	Maximum
WWU	56.77	34.78	91.96
W15U	67.29	12.28	95.70
AW3U	40.90	3.57	78.98
WWM	63.88	43.71	93.73
W15M	64.56	38.25	93.95
AW3M	57.99	30.44	86.27
REP	26.51	0.14	88.19

WWU = Weaning weight univariate; W15U = 15-month body weight univariate; AW3U = 3-year adult body weight univariate; WWM = Weaning weight multivariate; W15M = 15-month body weight multivariate; AW3M = 3-year adult body weight multivariate; REP = Repeatability model

The mean, minimum and maximum of the accuracies of the EBVs of all animals in the pedigree for WW, W15 and AW3 obtained with univariate, multivariate and repeatability animal models are presented in Table 10. EBVs for WWM, W15U and W15M had the highest mean accuracies, while EBVs obtained with the repeatability model had the lowest accuracy.

Discussion

It is important in any breeding program that the genetic and environmental components of variance for the traits under selection are known, in order to estimate accurate genetic parameters for incorporation in downstream applications. As far as the environmental effects are concerned, the year-season of birth had a significant effect on the weight of the animals throughout their lives. These differences in body weight could be ascribed to a range of factors, from maternal body condition score before mating to seasonal differences in grazing quality for mature animals. Male lambs were heavier than females, with a significant difference observed until 15 months of age. Single-born lambs were heavier at birth and W42, while single-raised lambs had a weight advantage from weaning until W15. The influence of non-genetic factors on growth traits corresponded to those reported in literature (Thiruvankadan et al., 2008; Boujenane & Diallo, 2017; Kumar et al., 2017; Jawasreh et al., 2018).

The Log L, AIC and BIC information criteria results were in agreement for all traits and based on these, the most suitable univariate model was identified for body weight at each age. Models incorporating both additive and permanent environmental maternal effects best described body weights up to 8 months of age. The magnitude of maternal effects highlighted the importance of accounting for these effects, as failure to do so will result in overestimation of heritability and unlikely expectations with regard to the rate of genetic progress that can realistically be achieved. Maternal variance was further partitioned into genetic and permanent environmental factors to better describe the dam environment's influence.

The moderate direct heritability of 0.20 ± 0.03 estimated with the univariate model for BW suggests that selection for this trait will be successful and corresponds to previously reported values of 0.18 (Safari et al., 2007a) to 0.35 (Wuliji et al., 2001) in Merino sheep. This estimate was also in line with parameters previously estimated in South African Merino sheep (Duguma et al., 2002; Cloete et al., 2003; Olivier, 2014). The permanent environmental maternal effect of 0.12 and maternal heritability of 0.11 estimated in this study indicates the importance of the maternal environment at birth, although

the additive maternal value was lower than most previous reports (Duguma et al., 2002; Cloete et al., 2003; Safari et al., 2007a; Olivier, 2014). Both maternal heritability and the permanent environmental maternal effect declined from birth to weaning.

The h^2_a estimate for W42 of 0.42 estimated in this study was above the range reported in literature for Merino pre-weaning weights (2 to 5 months of age), which ranged from 0.09 to 0.37 (Lewer et al., 1994; Mortimer & Atkins, 1995; Analla & Serradilla, 1998; Wuliji et al., 2001; Olivier, 2014). The h^2_m of 0.15, however, fell within the range previously reported.

The h^2_a of 0.16 for weaning weight estimated in this study was lower than most previous estimates for South African Merino sheep (Cloete et al., 2001 (0.18); Olivier et al., 2001 (0.21 and 0.30); Duguma et al., 2002 (0.26)), but higher than the 0.09 estimated by Olivier (2014) and 0.13 by Cloete et al. (2003). The lower direct heritability estimated in this flock compared to the other studies mentioned, could apart from genetic differences, most probably be ascribed to the impact of varying environmental conditions. The Grootfontein Merino stud was subjected to varying environmental conditions for the last 10 years of the recording period, with corresponding weaning weights ranging from 27 kg to 37 kg among the years.

At weaning, the maternal influence is still expected to be high. The relatively low maternal heritability of 0.04 obtained in this study was comparable to the lower end of the values reported for weaning weight in Merino sheep, while the maternal permanent environmental effect (0.09) was within the range previously reported (Snyman et al., 1996; Cloete et al., 2001; Wuliji et al., 2001; Duguma et al., 2002; Cloete et al., 2003; Olivier, 2014). Although weaning weight is lowly heritable in this stud and is influenced by maternal effects, it is an important trait that influence the economic viability of the enterprise as it directly contributes to income through an earlier marketing age and indirectly through the higher number of ewes that can be kept owing to the shorter production cycle.

The h^2_a (0.54 ± 0.15) and h^2_m (0.28 ± 0.17) estimated for W6 in this study were higher than the estimates reported in literature which ranged from 0.18 to 0.44 and 0.04 to 0.12, respectively (Snyman et al., 1996; Wuliji et al., 2001; Ingham et al., 2003; Olivier, 2014) on Merino sheep. Limited results are available for this age in previously published literature. However, the high parameter values obtained for W6 and W8 in this study is in contrast with the available literature reports and might have been influenced by incomplete W6 and W8 data. The relatively high standard errors for the estimates are evidence of this.

Heritability estimates reported for older post-weaning weights varies markedly with age of the animals (12 to 18 months), with a corresponding wide range of estimates. The heritability values for W12 (0.37) and W15 (0.51) corresponded to high values (0.47 and 0.49 respectively) reported by Olivier (2014) in South African Merino sheep. After 8 months of age, the magnitude of maternal effects declined rapidly. For W15 and adult weights from 3 years, the maternal effect was genetic rather than environmental.

The heritabilities estimated in this study differed from those estimated on this flock in previous studies (Olivier et al., 1994; Olivier et al., 2001). Direct (0.51 vs. 0.38) and maternal (0.08 vs. 0.01) heritabilities for W15 were higher than those estimated by Olivier *et al.* (1994), while direct heritability for WW was lower in the current study (0.16) than in the previous study (0.21) of Olivier et al. (2001). Genetic changes due to response to selection for body weight (Olivier et al., 1995) and different management practices most probably contributed to these differences.

Neither the univariate direct variance and heritability or the univariate maternal variance and heritability in this study show a specific trend, which is not in line with most reported results. In most flocks, direct variance and heritability increase with age from weaning onwards, while maternal variance and heritability decrease with an increase in age (Snyman et al., 1995; Vaez Torshizi et al., 1996; Ngere et al., 2017). However, the univariate phenotypic variance in this study did show an increase with age of the animal. The structure of the data and completeness of pedigree influence the model's ability to disentangle genetic and environmental effects (Gerstmayer, 1991; Maniatis & Pollott, 2003; Boligon et al., 2012). The limited number of records and incomplete dataset for W6 and W8 most probably impacted on these results.

Correlation estimates between direct and maternal genetic effects ranged from low negative at birth (-0.28) to high negative at 6 months of age (-0.95). The sign and magnitude of the direct-maternal correlation varies between different studies done on different breeds under different conditions. The majority of the reported estimates are negative for Merino sheep and ranged from -0.20 to -0.59 (Mortimer & Atkins, 1995; Vaez Torshizi et al., 1996; Olivier, 2014). Only two positive estimates of 0.05 (Duguma et al, 2002) and 0.57 (Snyman et al., 1996) could be found for Merino sheep. This negative correlation between the direct and maternal effects should be kept in mind when including early body weights in the breeding plan, as selection progress could be less than expected when only considering the heritabilities.

Multivariate additive variance components were higher than the univariate additive variance for a specific body weight and tended to increase with age of the animal. Direct heritabilities estimated with multivariate models were lower than the respective heritabilities obtained with univariate analyses for W12, W15 and AW3, but was the same for WW. Miraei-Ashtiani et al. (2007) reported similar direct heritabilities for BW, W6 and W12 with uni- and multivariate models, but a higher heritability for WW with the multivariate model. Including the traits in the multivariate model accounted for the direct as well as maternal genetic correlations among the traits. These genetic relationships among the traits consequently affected the genetic parameters estimated with the multivariate model.

Maternal genetic variance was lower when estimated with the multivariate model compared to the univariate model for WW (0.411 vs. 0.943) and W15 (0.419 vs. 2.693). The same applied for the maternal permanent environmental variance for W12, which decreased from 1.375 with the univariate model to 0.00 with the multivariate model. The corresponding multivariate variance ratios were also lower. Phenotypic variance of W12, W15 and AW3 were much higher with the multivariate model than with univariate analysis. This consequently led to higher multivariate residual variance components for these body weights.

With the multivariate model, direct genetic correlations of W15 with WW, W12 and AW3 were estimated at 0.83 ± 0.05 , 0.69 ± 0.05 and 0.76 ± 0.05 respectively. The strong positive genetic correlation between weights at different ages has been well described and was expected (Safari et al., 2007b; Olivier, 2014). Selection based on W15, as is currently the case in the South African Merino breed, will have a positive response on body weights at all other ages.

As with the univariate models, a combination of LogL, AIC and BIC information criteria were used to determine the most suitable repeatability model for each trait. The model without fitting splines was the most suitable model for estimating the (co)variance components and genetic parameters for body weight in this instance. The direct heritability for body weight using the repeatability model for this study was 0.26 ± 0.06 , which compared favourably with the average of the heritability estimates using multivariate analysis. The estimated repeatability of 0.37 for body weight from birth weight to 5 years of age was higher than the range of 0.19 to 0.26 reported in studies on three Canadian breeds (Hansen & Shrestha, 2002) and the Cradock fine wool Merino stud (Olivier, 2014). Estimates exceeding 0.46 were reported in several other studies (Hatcher *et al.*, 2005; Wolc *et al.*, 2011; Boujenane *et al.*, 2013).

The medium to high direct additive heritability estimates indicate that selection for growth traits can have positive results in a relatively short time. Both maternal direct and permanent environmental effects will influence these results. The negative correlation between direct and maternal additive genetic effects should be kept in mind, as it will slow down selection response.

The EBVs for body weight for Merino sheep obtained with the different models were compared using Spearman rank correlations, accuracy of EBVs, as well as the number and proportion of common animals in the Top 10% and Top 1% lists. The Spearman rank correlation was used to estimate the correlation between the ranking of animals on estimated breeding values for WW, W15 and AW3. When animals were selected on EBVs estimated with multivariate models, 92% of the animals selected on any of the body weights had the same ranking. This corresponds with the high genetic correlations estimated among WW, W15 and AW. Furthermore, when using the Top 1% lists, 95% and 94% of the animals selected on either uni- or multivariate EBVs for W15 and WW respectively, would be identical. The highest accuracies for EBV were also calculated for univariate and multivariate WW and W15 analyses. However, if selection is based on univariate W15 EBVs, the possibility is greater that different animals will be selected, due to the lower rank correlation of W15U with WWU (0.67) and WWM (0.80) respectively. EBVs estimated with the repeatability models is unsuitable for use, as these had the lowest accuracies and there will be major re-ranking of animals when repeatability model EBVs and any of the other EBVs are used. No comparable literature reports on comparison of EBVs of body weights of sheep with different statistical models could be found.

Conclusion

The moderate to high estimates of heritability for body weight demonstrated that although being subjected to selection for increased body weight for many years, there is still considerable additive genetic variation in body weight available in this study. Body weights up to 8 months of age were influenced by maternal additive and permanent maternal environmental effects. The significant maternal effects for early body weights confirm that it must be included in the models for estimation of breeding values. The results of the present study indicate that the multivariate model is the most appropriate model for estimating breeding values for body weight at selection age in the Grootfontein Merino stud.

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