Variance component and heritability estimates of early growth traits in the Elsenburg Dormer sheep stud

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A total of 8 909 birth weight and 7 740 weaning weight records, from the progeny of 215 sires, collected from 1943 to 1990 from the Elsenburg Dormer sheep stud, were analysed. Additive genetic variance and heritability estimates for birth weight (BW), weaning weight (WW), average daily gain (ADG) and the Kleiber ratio (KL) were obtained by Restricted Maximum Likelihood (REML) procedures fitting three different models. Estimates were severely biased upwards when an animal model, ignoring maternal effects, was fitted. A sire model yielded more realistic estimates of direct additive variance. Estimates of maternal genetic variance and corresponding heritabilities (h^2_m) were higher than estimates for direct additive variance and heritability (h^2_a) when fitted simultaneously in an animal model. The genetic correlations between direct and maternal influence were consistently negative but the proportion of cov (a, m) to phenotypic variance decreased from birth to weaning. The heritability estimates were as follows: BW = 0.12, 0.42, 0.16, 0.43; WW = 0.12, 0.34, 0.13, 0.20; ADG = 0.13, 0.31, 0.13, 0.18; KL = 0.13, 0.26, 0.14, 0.14 for a sire model, animal model, animal model direct effects (h^2_a) and animal model maternal effects (h^2_m), respectively.

'n Totaal van 8 909 geboortegewig- en 7 740 speengewigrekords van die nageslag van 215 ramme, wat vanaf 1943 tot 1990 by die Elsenburg Dormerskaapstoet ingesamel is, is ontleed. Additiewe genetiese variansie en oorerflikheids-beramings van geboortegewig (GW), speengewig (SW), gemiddelde daaglikse toename (GDT) en die Kleiberverhou-ding (KV) is met behulp van Beperkte Maksimum Aanneemlikheid(REML)-prosedures beraam deur drie verskillende modelle te pas. Beramings was onrealisties hoog met die passing van 'n dieremodel ('animal model') sonder moedereffekte. Meer realistiese beramings van direkte additiewe variansie is met behulp van 'n vaarmodel ('sire model') verkry. Beramings van maternale genetiese variansie en ooreenstemmende oorerflikhede (h^2_m) was hoër as dié van direkte additiewe variansie en oorerflikheid (h^2_a). Die genetiese korrelasies tussen direkte invloed en moeder-invloed was deurgaans negatief, maar die proporsie van maternale genetiese variansie tot fenotipiese variansie het van geboorte tot speen afgeneem. Die beraamde oorerflikhede (h^2) was soos volg: GW = 0.12, 0.42, 0.16, 0.43; SW = 0.12, 0.34, 0.13, 0.20; GDT = 0.13, 0.31, 0.13, 0.18; KV = 0.13, 0.26, 0.14, 0.14 vir 'n vaarmodel, dieremodel en dieremodel met moedereffekte (h^2_a en h^2_m), onderskeidelik.

Keywords: Dormer sheep, heritability, maternal effect, REML, variance components.

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Introduction

Early growth traits are important factors influencing the profitability of any sheep meat production enterprise. Some of these traits have been recommended as selection criteria for meat production in sheep (Anon, 1970; Olson *et al.*, 1976; Lasslo *et al.*, 1985; Badenhorst *et al.*, 1991). If these traits are to be included in a breeding programme, accurate estimates of breeding values will be needed to optimize selection programmes. This requires a knowledge of variance and co-variance components.

In recent years, heritability estimates of growth traits have been reported for many breeds of sheep. However, little information is available on heritabilities for these traits in Dormer sheep (Van der Merwe, 1976). Most of the reported heritabilities are based on ratios of variance components estimated mainly by Henderson's Method 3. Over the last decade, Restricted Maximum Likelihood (REML) (Patterson & Thompson, 1971) has become the method of choice for estimating variance components because of its desirable properties (Harville, 1977). Sorenson & Kennedy (1984), Meyer & Thompson (1984) and Walter & Mao (1985) have

shown that, if the information on which selection was based is included in the analysis, REML will yield estimates that are unbiased by selection. However, while the variance components may be unbiased, their ratios (heritabilities) may still be biased.

An important advantage of REML, utilizing relationships, is that the assumptions that animals (sires) are unrelated and are non-inbred, need not be made. Such assumptions are unrealistic where the level of inbreeding is known to be high, as in the present study (Van Wyk *et al.*, 1993).

A complication that arises, especially with early growth traits, is that the traits may be influenced by direct genetic effects and maternal genetic effects. This implies that selection can be for direct performance or maternal performance or for both. The relative magnitudes of direct and maternal additive variances as well as the genetic correlations between them, need to be known.

The purpose of this study was to estimate variance components and heritabilities for early growth traits in the Elsenburg Dormer stud by fitting three possible descriptive mixed models for REML estimates.

Material and Methods

Data were obtained from the registered Dormer stud comprising a flock of 180 breeding ewes at the Elsenburg Experimental Farm near Stellenbosch. A detailed description of the genetic base (history), selection criteria and management of the stud is given by Van Wyk *et al.* (1993).

The sheep used in the analyses were born in the period 1943 to 1990. A total of 8 909 birth weight and 7 740 weaning weight records, from the progeny of 215 sires, were available after editing. The data were edited to exclude the following:

(i)   sires with less than seven progeny,
(ii) records from years 1941 and 1942,
(iii) records of stillborn lambs, and
(iv) incomplete records.

Flock management was designed to ensure uniform treatment as far as practically possible. Each ram was paddock-mated with 25—30 indentified ewes. Limited cross-fostering of orphaned lambs apparently did take place and may have some effect on the validity of the data. This, however, is a universal problem in sheep breeding research and it is almost impossible to control cross-fostering effectively.

Statistical analysis

Three different mixed linear models were used to describe the data. The first model is as follows:

$$y = Xb + Zr + e \qquad (1)$$

where y is a vector of progeny records for birth weight (BW), weaning weight (WW), average daily gain from birth to weaning (ADG) and Kleiber ratio (ADG/WW$^{0.75}$) (KL), b is a vector of fixed effects consisting of year-season of birth, age of dam, sex of lamb, birth status of progeny and inbreeding subclass as identified by Van Wyk *et al.* (1993), r is a random vector associated with the additive genetic effect of rams, and e is a random vector associated with residual errors. This is therefore a 'sire' model. Variance-covariance matrices of the parameters were assumed to have the following structure:

$Var(r) = A\sigma^2_r$, $Var(e) = I\sigma^2_e$, and $Var(y) = ZAZ'\sigma^2_r + I\sigma^2_e$ where A is a numerator relationship matrix, I is an identity matrix, and σ^2_r and σ^2_e are ram and residual variance components, respectively. The matrix A was calculated from ram pedigrees only using the method of Quaas (1976). This implies that inbreeding coefficients could not be calculated properly. Since preliminary analyses showed a relatively high level of inbreeding in these data, it was decided to include the level of inbreeding as a fixed effect. A detailed description of all fixed effects included in this study is given by Van Wyk *et al.* (1993).

The variance components for rams and residuals were estimated by REML procedure, using the algorithm described by Konstantinov & Erasmus (1992). No convergence criterion was set.

The second model used was an 'animal' model:

$$y = Xb + Za + e \qquad (2)$$

This model differs from (1) with respect to the matrix $Z = I$ and the vector a which denotes a random vector for the animal's own additive genetic effect. Additionally, inbreeding was excluded from vector b but included in A. It was assumed that:

$Var(a) = A\sigma^2_a$, $Var(e) = I\sigma^2_e$, and $Var(y) = ZAZ'\sigma^2_a + I\sigma^2_e$

where σ^2_a and σ^2_e is the additive genetic variance and environmental variance, respectively. The relationship matrix was constructed using full pedigree information and inbreeding was taken into account, hence its exclusion from vector b. The third model considered, was as follows:

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

This model differs from (2) only with respect to the random part. The matrix Z was partitioned into two parts, viz. $Z_1 = Z_2 = I$, as well as the corresponding vector $a = [a, m]$, where a is a random vector of direct additive genetic effects of the animals, and m is a random vector of the maternal additive genetic values. The rest of the parameters are the same as in (2).

The variance-covariance matrices were assumed to have the following structure:

$Var(a) = Z_1AZ'_1\sigma^2_a$, $Var(m) = Z_2AZ'_2\sigma^2_m$,

$Cov(a, m) = Z_1AZ'_2\sigma_{am}$ and $Var(e) = I\sigma^2_e$ with

$Var(y) = Z_1AZ'_1\sigma^2_a + Z_2AZ'_2\sigma^2_m + Z_1AZ'_2\sigma_{am} + I\sigma^2_e$

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

The variance-covariance components under models (2) and (3) were estimated by derivative-free REML (DFREML), using the program of Meyer (1989; 1991). The convergence criterion was the variance of the function values. A value of 10 was used which, according to Meyer (1991), gives a good accuracy of estimation. Analyses were carried out using the Simplex method as suggested by Meyer (1989).

Starting values for iterations were obtained from preliminary analysis using Henderson's Method 3 from Harvey's LSMLMW computer program (Harvey, 1988).

Heritabilities for additive genetic effects were estimated as follows:

(i)   sire model
      $h^2 = 4\sigma^2_s / (\sigma^2_s + \sigma^2_e)$

(ii) animal model
      $h^2 = \sigma^2_a / (\sigma^2_a + \sigma^2_e)$

From Model 3, different heritabilities can be estimated. According to Willham (1963; 1972), the effect of a dam W on individual X can be illustrated by the path diagram shown in Figure 1.
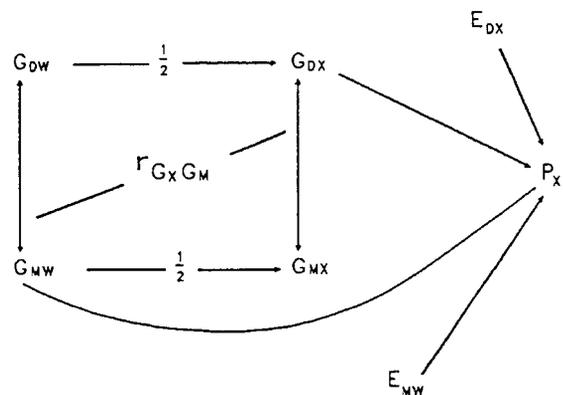
Figure 1 A path diagram describing a phenotypic value influenced by a maternal effect (after Willham, 1972).

In Figure 1, P_X denotes the phenotype of individual X; E_{DX} is the non-maternally caused environmental effect; G_{DX} is the direct additive genetic effect of X; G_{MX} is the genetic maternal ability of X which is not measured; G_{MW} is the genetic maternal effect of X; G_{DW} is the genetic effect associated with the dam of X; and E_{MW} is the environmental maternal effect on X.

According to Willham's model, an individual X has two additive genetic values, one for component D that is expressed in P_X and one for component M that will be expressed only if X subsequently becomes a dam (Willham, 1963). The fraction of the genetic selection differential that would be realized if selection were on P is defined as the regression of (G_{DX} + G_{MX}) on P_X (Willham, 1972) with the covariance term as:

$$\text{Cov}(G_{DX} + G_{MX}), P_X = \sigma^2_{G_{DX}} + \tfrac{3}{2}\sigma_{G_{DX}G_{MX}} + \tfrac{1}{2}\sigma^2_{G_{MX}}$$

Thus, from Model 3, the phenotypic variance was estimated as:

$$\sigma^2_p = \sigma^2_a + \tfrac{3}{2}\sigma_{am} + \tfrac{1}{2}\sigma^2_m + \sigma^2_e$$

and, utilizing the different variance components, three different heritabilities were estimated:

(i) Heritability for the direct additive genetic effect:

$$h^2_a = \sigma^2_a / \sigma^2_p$$

(ii) Heritability for the maternal effect:

$$h^2_m = \sigma^2_m / \sigma^2_p$$

(iii) Heritability for the total genetic effect, i.e. the value used to calculate expected response to phenotypic selection:

$$h^2_T = (\sigma^2_a + \tfrac{3}{2}\sigma_{am} + \tfrac{1}{2}\sigma^2_m) / \sigma^2_p$$

The genetic correlation between the direct additive and maternal additive genetic effects was estimated as:

$$r_{Gam} = \sigma_{am} / (\sigma^2_a \sigma^2_m)^{1/2}$$

All calculations were performed on a Convex computer Model C 120.

Results and Discussion

The variance components along with the heritabilities of the traits studied, estimated from the sire model, are presented in Table 1. The estimates of heritabilities for BW, WW and ADG are lower than most of the values reported in the literature but correspond to those reported by Van der Merwe (1976) for Dormer sheep. The estimate of heritability for KL agrees with the results reported by Badenhorst et al. (1991). The differences in values of heritabilities might be ascribed to the different estimation procedures used, different breeds of

sheep, or different data sets. There might also be a genetic reason for the low additive heritabilities, such as a maternal effect. The sire model used did not take into account all relationships between animals, but the individual animal model fitted (Model 2) did, and the results are shown in Table 2. The estimates of additive genetic variance as well as heritabilities for all traits studied were considerably higher than those obtained from the sire model. These results clearly suggest a large maternal effect on the traits under consideration. Both additive genetic variance and heritability estimates were undoubtedly biased upwards. Maternal effects were probably confounded with animal effects. Similar findings with Tribolium are reported by Berger (1991).

To examine this potential bias, the animal model with maternal effects included (Model 3), was fitted. The variance components and heritabilities obtained are presented in Table 3.

The estimates of the additive genetic variance as well as the direct heritabilities were reduced considerably. Except for KL, the estimates of the maternal genetic variance and h^2_m

Table 1 Estimates of variance components and heritabilities from REML (sire model)

Parameters	Traits[a]			
	BW	WW	ADG	KL
σ^2_s	0.0139	0.6610	63.8671	0.0576
σ^2_e	0.4474	21.4563	1966.3041	1.6865
σ^2_p	0.4613	22.1173	2030.1712	1.7441
h^2	0.1205	0.1195	0.1258	0.1321

[a] BW = birth weight; WW = weaning weight; ADG = average daily gain; KL = Kleiber ratio.

Table 2 Estimates of variance components and heritabilities from DFREML (animal model)

Parameters	Traits[a]			
	BW	WW	ADG	KL
σ^2_a	0.2264	8.3339	693.7701	0.4889
σ^2_e	0.3104	16.1447	1527.0807	1.3820
σ^2_p	0.5368	24.4786	2220.8508	1.8709
h^2	0.4217	0.3405	0.3124	0.2613
$\pm SE$	0.0218	0.0295	0.0299	0.0304

[a] BW = birth weight; WW = weaning weight; ADG = average daily gain; KL = Kleiber ratio.

Table 3 Estimates of variance components and heritabilities for additive direct (a) and maternal (m) effects for birth weight (BW), weaning weight (WW), average daily gain (ADG) and Kleiber ratio (KL) in Dormer lambs (animal model with maternal effects)

Parameters	Traits			
	BW	WW	ADG	KL
σ^2_a	0.091925	3.07073	283.72787	0.25538
σ^2_m	0.24788	4.81751	385.35769	0.25151
σ_{am}	−0.05249	−0.60214	−56.25141	−0.06326
σ^2_e	0.28609	16.80000	1555.29507	1.42143
σ^2_p	0.57341	24.08610	2168.12922	1.86506
h^2_a	0.1603	0.1275	0.1309	0.1369
$\pm SE$	0.0279	0.0281	0.0245	0.0269
h^2_m	0.4323	0.2000	0.1777	0.1349
$\pm SE$	0.0284	0.0300	0.0298	0.0223
h^2_T	0.2391	0.1899	0.1808	0.1535
σ_{am} / σ^2_p	−0.0915	−0.0250	−0.0259	−0.0339
$\pm SE$	0.0286	0.0230	0.0116	0.0263
r_{Gam}	−0.3477	−0.1566	−0.1701	−0.2496

were larger than estimates of σ^2_a and h^2_a. In beef cattle the opposite is frequently reported (Koch, 1972; Philipsson, 1976; Burfening et al., 1981; Bertrand & Benyshek, 1987; Trus & Wilton, 1988). Khaldi & Boichard (1991) also reported lower maternal heritabilities for birth weight and live weight at 10, 20 and 90 days of age in Barbary sheep. However, in Dormer sheep the higher maternal variances and heritabilities for the traits studied could be attributed to the large proportion of multiple births. Single-born lambs constituted only 36.02% of all lambs born while twins and triplets made up 59.93% and 4.05%, respectively.

There was a consistent trend for r_{Gam} to be negative for all traits studied. The average value reported in the literature for beef cattle is –0.65 (Cantet et al., 1988). Khaldi & Boichard (1991) found the genetic correlation between direct and maternal effects to be within the range of –0.04 to –0.62 for early growth traits in sheep. The large negative r_{Gam} implies that improvement in one effect will lead to a reduction in the other. Riska et al. (1985) suggested that there is a higher correlation between direct and maternal effects at later stages of growth. They also suggested that changes in σ_{am} during growth are more likely to be affected by changes in the direct than the maternal effect component. These results are not supported in this study. The proportion of σ_{am} to the phenotypic variance was 9.15% and 2.5% for BW and WW, respectively.

The results in this study showed that different estimates of heritabilities can be obtained for early growth traits in Dormer sheep using a REML estimation procedure but applying different models. Therefore, model specification plays an important role in the accuracy of estimation. This is true for all types of traits, but it becomes of vital importance when traits, which could have been influenced by maternal effects, have to be analysed.

The estimates of variance components and heritabilities obtained using a sire model (Model 1) are closer to the values obtained using the animal model with maternal effects (Model 3) than to those estimated from an individual animal model with maternal effects excluded (Model 2). This is very important if selection has to be made on direct breeding value alone. Using the estimates of heritabilities from Model 2, one could expect improved rates of response by selection on direct additive genetic value. However, the results from the analysis using Model 3 showed that the direct additive genetic variation is lower compared to the maternal genetic effect.

It is interesting to ascertain whether the response to selection will be greater if selection is made on both direct and maternal breeding values rather than on direct breeding value alone. This is of importance particularly in creating dam lines in which increased selection pressure is placed on these specific traits.

The estimates of the total heritabilities suggest that the response to selection on phenotype would be slow because of the negative genetic correlation between direct and maternal effects.

In this analysis, common environmental effects were not taken into account. Variance components may therefore be biased owing to unaccounted environmental covariances. As was pointed out by Shaw (1987), the error effects contributing to the phenotype of the individual would then not be independent. Another source of possible bias in maternal components is a possible genetic effect of dams owing to dominance. A further study is under development to assess this possible source of genetic variation.

Although the animal model used allows simultaneous estimation of direct and maternal variances, it was far more demanding than the sire model with respect to CPU time used. For BW, 200 iterations were carried out and the CPU time was more than 30 min. The iterations needed to reach convergence for the rest of the traits varied between 55 and 220 with an average CPU time of 40 min. The CPU time used for the sire model was negligable owing to the diagonalization of the coefficient matrix as noted by Konstantinov & Erasmus (1992).

Conclusions

Maternal effects had an appreciable influence on all traits studied in this Dormer stud. The direct additive genetic variances and heritabilities estimated from an animal model with maternal effects excluded were severely biased upward. If selection is to be made on direct effects alone, breeding values based on the estimates of the variance components under a sire model are preferable to those from an animal model accounting for direct effects only. The sign of σ_{am} was negative for all traits studied. The value of r_{Gam} for BW was smaller than for the other traits under consideration. A practical implication of this finding is the reduction in the expected response to selection for BW, as theoretically shown by Van Vleck et al. (1977). This negative influence seemed to be smaller for the rest of the traits studied.

Acknowledgements

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