

Multitrait Estimates of (Co)Variance Components and Genetic Parameters of Prewaning Growth Traits in a Multibreed Beef Cattle Herd

Hailu Dadi¹, S.J. Schoeman², G.F. Jordaan²

¹Adami Tulu Reseach Center, P.O.Box 35, Ziway, Ethiopia

²Department of Animal sciences, University of Stellenbosch, Private Bag X1, Matieland, 7602, South Africa.

Abstract

Variance components and resulting genetic parameters of birth weight (BWt), weaning weight (WWt) and average daily gain (ADG) in a multibreed beef cattle population were estimated by Restricted Maximum Likelihood (REML) procedures based on 4117 records. Four multitrait animal models were fitted including a simple model with the animal direct effects as the only random effect and another model allowing for both genetic and permanent maternal environmental effects. The model that included direct genetic and permanent maternal environmental effects generally best described the data analysed. The simple model ignoring maternal effects most likely inflated direct heritability estimates. Direct heritability estimates were 0.11, 0.19, and 0.15 for BWt, WWt and ADG, respectively using a model comprised both the genetic and maternal environmental effects. Maternal heritabilities were low under both Model 3 (accounted for direct and maternal genetic effects) and 4 (direct and maternal genetic and permanent maternal environmental effects), ranging from 0.02 to 0.26. Permanent maternal environmental effects were the important factor sdetermining WWt and ADG. Direct and maternal genetic correlations ranged from 0.42 to 0.44 (BWt), -0.22 to -0.25 (WWt) and -0.17 to -0.23 (ADG).

Keywords: Beef cattle, preaweaning traits, direct heritability, maternal heritability, total heritability, genetic correlation

Introduction

The potential for genetic improvement in economically important traits of beef cattle in a selection programme depends on the extent of the genetic variation, heritability and sign and magnitude of genetic correlations of the traits considered. Several estimates of maternal heritabilities and direct-maternal genetic correlations in the past have been obtained by calculating

variance component estimates from sire-maternal-grand-sire and sire-dam models analyses (Quaas, *et al* 1985; Trus and Wilton, 1988; Brown *et al.*, 1990; Wright *et al.*, 1991). However, owing to the recent increased computing power available, linear models are employed in the genetic evaluation of animals separating direct genetic, maternal genetic and maternal permanent environmental effects, using animal models (Mackinnon *et al.*, 1991; Meyer, 1992a; Swalve, 1993; Robinson, 1996b; Schoeman and Jordaan, 1999). In general, the animal model is considered the preferred model for a wide range of applications. A number of investigations applied this methodology for unitrait analysis of early growth traits of beef cattle, but, to date, limited estimates have been reported from corresponding multitrait analyses for multibreed beef cattle.

Genetic parameters for the traits of interest are a characteristic of the population in which they are estimated. Their estimates vary widely between authors, years, methods of estimation, breeds and production systems (Mohiuddin, 1993; Swalve, 1993; Koots *et al.* 1994a; b; Robinson, 1996a). The objective of this work therefore was to estimate (co)variances, heritabilities and genetic correlations for preweaning growth traits in a multibreed beef cattle by separating direct genetic, maternal genetic and maternal permanent environmental effects fitting multitrait animal models.

Materials and Methods

Data were obtained from multibreed beef calves born and raised on the Johannesburg Metropolitan Council's farms during the period of 1968 to 1992. The beef herds have been kept on two farms, *viz.* the Olifantsvlei farm and the Northern farm, which are located in the Gauteng province of South Africa. The beef herds are raised on a restricted pasture feeding system using irrigated annual and perennial rye grass pastures supplemented with *Eragrostis curvula* hay, maize meal, distillers grain and silages of maize, sorghum and grass (Paterson *et al.*, 1980) when necessary. Breeding systems, animal management and selection procedures of the herd were described in detail by Schoeman and Jordaan (1999).

Birth weight, birth date, weaning weight and weaning date as well as breed identity were recorded for each individual calf born during this period. Breed identity of each animal was established by tracing pedigrees back to the base population. Cows calved almost throughout the year; however, the majority (67%) of calves were born in winter (June - October). Hence, season of birth

was recorded as either "summer born" or "winter born". After editing the data by removing extreme values of weights and calves with unknown parents, 4119 records were available for analysis. The records included birth weight (BWt), weaning weight (WWt) and pre-weaning average daily weight gain (ADG). The characteristics of the dataset are presented in Table 1.

Table 1 Characteristics of the data set for BWt, WWt and ADG (birth to weaning) of calves.

	Number of records	Minimum	Maximum	Mean	Standard deviation
Birth weight (kg)	4119	22.00	55.00	35.80	6.20
Weaning weight (kg)	4119	102.00	358.00	192.40	34.89
Average daily gain (kg)	4119	0.28	1.92	0.75	0.14
Calf age at weaning (days)	4119	106.00	310.00	210.70	26.90
Dam age at parturition (years)				5.64	2.30
Number of calves/sire				56.40	
Number of calves/dam				2.10	

Statistical procedures

First the data set was analysed using the General Linear Model (GLM) procedures of the Statistical Analysis Systems (SAS, 1996). The variables fitted included the fixed effects of dam age (4 levels), genotype of calf (58 levels), sex of calf (2 levels) and herd-year-season (66 levels). Weaning age of calf was included as a covariate for WWt. All fixed effects and their interactions that had no ($P > 0.05$) influence on BWt, WWt and ADG were excluded from the final analysis using the step down elimination procedure.

Estimates of (co)variance components from and multitrait analyses were then performed by using the REML VCE packages of Groeneveld (1996, 1997), fitting four animal models. Model 3 and 4 allowed for a covariance between direct and maternal genetic effects. These models in matrix notation were:

$$\text{Model 1: } Y = Xb + Z_1a + e \quad \text{Model 2: } Y =$$

$$Xb + Z_1a + Z_2c + e \quad \text{Model 3: } Y = Xb + Z_1a +$$

$$Z_2m + e$$

$$\text{Model 4: } Y = Xb + Z_1a + Z_2m + Z_3c + e$$

Where :

Y = a vector of the calf's record for each trait.

X = a known incidence matrix relating the observations to the fixed effects.

\mathbf{b} = a vector of fixed effects

Z_1, Z_2 and Z_3 = known incidence matrices relating the observation (Y) to the unknown random effects of \mathbf{a} , \mathbf{m} and \mathbf{c} .

\mathbf{a} = denotes a random vector for the animals own additive genetic effects.

\mathbf{m} = a random vector of maternal additive genetic effects

\mathbf{c} = a random vector of permanent maternal environmental effects

\mathbf{e} = a vector of random residual errors.

It is furthermore assumed that:

$\text{Var}(\mathbf{a}) = \mathbf{A}\sigma_a^2$, $\text{Var}(\mathbf{m}) = \mathbf{A}\sigma_m^2$, $\text{Var}(\mathbf{c}) = \mathbf{I}\sigma_c^2$, $\text{Var}(\mathbf{e}) = \mathbf{I}\sigma_e^2$, $\text{Cov}(\mathbf{a}, \mathbf{m}) = \mathbf{A}\sigma_{am}$

Where, \mathbf{A} = the numerator relationship matrix between the animals

σ_a^2 = the direct additive genetic variance

σ_m^2 = the maternal additive genetic variance

σ_c^2 = the variance of maternal permanent environmental effects

σ_e^2 = the variance of residual error

σ_{am} = the genetic covariance between direct and maternal genetic effects

\mathbf{I} = an identity matrix.

Heritabilities were estimated as follows: (a) Heritability for the direct additive genetic effects, $h^2_a = \sigma_a^2 / \sigma_p^2$, where σ_p^2 is the phenotypic variance;

(b) Heritability for the maternal genetic effects, $h^2_m = \sigma_m^2 / \sigma_p^2$; (c) Total heritability, $h^2_T = [\sigma_a^2 + 0.5\sigma_m^2 + 1.5\sigma_{am}] / \sigma_p^2$, (Willham, 1972). The genetic correlation between direct and maternal genetic effects was estimated by:

$$r_{am} = \sigma_{am} / (\sigma_a^2 \sigma_m^2)^{1/2}$$

Result and Discussions

Estimates of (co)variance components and total heritabilities (h^2_T) are presented in Table 2 while estimates of h^2_a , h^2_m , permanent maternal environmental effect (c^2), direct genetic correlations and maternal genetic correlations are presented in Table 3 for BWt, WWt and ADG from multitrait analysis. Estimates of heritabilities for all traits agreed with the values in the

literature summarised by Meyer (1992a), although the estimates reported varied according to the differences in type of records analysed (Wright *et al.*, 1987), methods of estimation (Nelsen *et al.*, 1986) and models used for the analysis (Mohiuddin, 1993). According to log likelihood value (Groeneveld, 1996; 1997) Model 2 provided a better fit to the data for all traits. The h^2_T estimates varied from 0.15 to 0.59. Total heritability estimates for the traits lie within the range of literature estimates of Mohiuddin (1993), which vary from -0.02 to 0.68 for BWt and from 0.02 to 0.81 for WWt. Estimates of h^2_T for ADG also correspond with literature estimates reported in the review of Meyer (1992a).

Table 2 Estimates of (co)variance components (kg²) and total heritabilities (h^2_T) of BWt, WWt and ADG.

Model	Parameters						
	σ^2_A	σ^2_m	σ_{am}	σ^2_c	σ^2_e	σ^2_p	h^2_T
Birth weight							
Model 1	15.03				10.41	25.44	0.59
Model 2	5.79			3.49	13.89	23.17	0.25
Model 3	2.40	3.37	1.24		15.70	22.71	0.26
Model 4	2.57	2.37	1.02	1.25	15.47	22.68	0.23
Weaning weight							
Model 1	346.64				331.10	677.74	0.51
Model 2	114.24			137.84	376.81	628.89	0.18
Model 3	114.93	158.95	-29.27		389.09	633.70	0.26
Model 4	119.18	21.61	-12.58	128.31	372.65	629.17	0.18
Average daily gain							
Model 1	0.007				0.007	0.014	0.48
Model 2	0.002			0.003	0.008	0.013	0.15
Model 3	0.002	0.003	0.000		0.009	0.014	0.25
Model 4	0.002	0.000	0.000	0.003	0.008	0.013	0.15

σ^2_a direct additive genetic variance; σ^2_m maternal additive genetic variance; σ_{am} direct-maternal genetic covariance; σ^2_c maternal permanent environmental variance; σ^2_e error variance; σ^2_p phenotypic variance; h^2_T total heritability.

The direct heritabilities (h^2_a) were high under Model 1, while they were low to medium under the alternative models (Table 3). The exclusion of the maternal effects most likely inflated h^2_a for all traits. The results of Model 1 that yielded high heritabilities in this study agree with Mackinnon *et al.* (1991) who reported h^2_a estimates of 0.78 (BWt), 0.56 (WWt) and 0.50 (ADG)

in tropical cattle when fitting a model accounting for direct genetic effects only. Schoeman and Jordaan (1999) found h^2_a estimates of 0.62 for BWt and 0.52 for WWt in the same multibreed beef cattle herd but using a different subset of the data and fitting a multitrait animal model, which accounted for direct effects only. To assess this potential bias in the present study, either a maternal permanent environmental effect (Model 2) or maternal additive genetic effect (Model 3) or both (Model 4) were included in the models, and the resultant h^2_a estimates were considerably reduced (Table 3).

The present estimates of h^2_a for BWt and WWt were lower than the unweighted means reported by Koots *et al.* (1994a) for BWt (0.35) and WWt (0.27) when fitted to Models 2, 3 or 4.

The direct genetic correlations (r_g) (Table 3) varied from 0.37 to 0.97 for the traits, indicating a medium to high genetic association between them. The correlation between the direct genetic components of BWt and WWt were larger than those between BWt and ADG under all the models. The correlations between WWt and ADG for the different models were high and almost unity. Although the correlations between the traits were all positive, differences were observed in estimates between the models. As indicated by Meyer (1992b), the differences in estimates between the different models may be related to the inclusion of environmental covariances or possible negative sampling correlations and large sampling errors. Mackinnon *et al.* (1991) Reported direct genetic correlations between BWt and WWt, BWt and ADG, and WWt and ADG of 0.43, 0.24 and 0.94, respectively. Likewise, Koots *et al.* (1994b) reported similar mean positive genetic correlations between BWt and WWt (0.50) and BWt and ADG (0.26). The results of this study as well as those in the literature suggest that selection for higher WWt or ADG would increase BWt, which may be associated with dystocia and loss of productivity. Because of such genetic relationships, other selection criteria should be sought when the objective is to increase WWt without adversely affecting BWt in such a herd. For example, Schoeman and Jordaan (1999) suggested an index of cow efficiency as the best appropriate selection criteria when the aim is to improve WWt without a corresponding increase in BWt.

Maternal heritabilities (h^2_m) varied from 0.02 in Model 4 to 0.26 in Model 3 (Table 3). The inclusion of the maternal environmental effect (c^2) in Model 4 reduced the h^2_m estimates for all traits compared to estimates with Model 3. However, in the study of Schoeman and Jordaan (1999), the inclusion of c^2

had almost no effect on h^2_m estimates of pre-weaning related traits, except for pre-weaning relative growth rate. These estimates are in agreement with the results of Mostert *et al.* (1998) who found h^2_m estimates of 0.06 to 0.15 for BWt and 0.08 to 0.19 for WWt fitting a multitrait model accounting for both direct and maternal effects in five beef cattle breeds in South Africa. Koots *et al.* (1994a) also reported a weighted mean h^2_m of 0.14 for BWt and 0.13 for WWt.

Maternal genetic correlations (Table 3) were all positive, and ranged from a low of 0.04 between maternal components of BWt and ADG to a high of 0.99 between WWt and ADG. Apart from the correlation between WWt and ADG, all these maternal correlations were lower than the corresponding direct genetic correlations. Generally, the maternal genetic components of related traits are expected to be positively correlated. The correlation between BWt and WWt obtained from Model 4 is in agreement with those of Swalve (1993) who estimated maternal genetic correlations ranging from 0.30 to 0.83 in the Australian Simmentaler beef cattle. The Model 3 estimate of this parameter was somewhat lower than the weighted mean value in literature of 0.39 between BWt and WWt but agree with the value from Model 4 (Koots *et al.*, 1994b). The correlation between maternal effects for BWt and WWt reported by Rust *et al.* (1998) was 0.24 for the Semmentaler cattle population in South Africa.

The maternal permanent environmental effect (c^2) slightly varies between Models 2 and 4 for BWt, but was almost similar for WWt and ADG (Table 3). For BWt (Model 4), h^2_m tended to be slightly higher than c^2 . This is in agreement with previous findings of Meyer (1992a, 1993b) for Hereford and Angus beef cattle and Swalve (1993) for Simmentaler. Maternal heritabilities were lower than c^2 for WWt and ADG (Model 4). The results correspond with the estimates of Waldron *et al.* (1993) and Meyer (1993a) but varied from the reports of Bertrand and Benyshek (1987), Swalve (1993) and Schoeman and Jordaan (1999). Estimates of c^2 have tended to be higher in most studies using field data, like in this study. For instance, in Polled Hereford and Charolais field data Meyer (1993a; b) estimated c^2 for WWt from animal model to be 0.22 and 0.23, whereas h^2_m estimates were 0.10 and 0.04, respectively. The maternal permanent environmental effect plays an important role in the preweaning growth traits of this beef cattle population.

Table 3. Estimates of direct heritabilities (h^2_a) (left, on diagonal) and maternal heritabilities (h^2_m) (right, on diagonal) and permanent maternal environmental effect (c^2) (right, on diagonal in bracket), direct genetic correlations (left, above diagonal), maternal genetic correlations (right, above diagonal) from multitrait analyses of BWt, WWt and ADG fitting different animal models.

	Direct components			Maternal components		
	BWt	WWt	ADG	BWt	WWt	ADG
BWt						
Model 1	0.59	0.55	0.37			
Model 2	0.25	0.76	0.58	(0.15)*		
Model 3	0.10	0.69	0.49	0.14	0.17	0.04
Model 4	0.11	0.69	0.48	0.10	(0.05)	0.41
WWt						
Model 1		0.51	0.97			
Model 2		0.18	0.96		(0.22)	
Model 3		0.19	0.96		0.26	0.99
Model 4		0.19	0.95		0.04	(0.21)
ADG						
Model 1			0.48			
Model 2			0.15			(0.22)
Model 3			0.14			0.21
Model 4			0.15			0.02

* Permanent maternal environmental effect

Table 4. Correlations between direct genetic and maternal genetic effects and cross-correlations for BWt, WWt and ADG fitting Model 3 and 4.

	Traits	Direct genetic effect		
		BWt	WWt	ADG
Maternal Genetic effect	BWt			
	Model 3	0.44	0.72	0.78
	Model 4	0.42	0.77	0.84
	WWt			
	Model 3	-0.12	-0.22	-0.12
	Model 4	-0.23	-0.25	-0.11
	ADG			
	Model 3	-0.15	-0.26	-0.17
Model 4	-0.35	-0.43	-0.23	

The correlation between the direct genetic and maternal genetic effects (r_{am}) and cross-correlations among traits are presented in Table 4. These correlations were positive for BWt but negative for WWt and ADG. These estimates for BWt were larger than literature reports of Mohiuddin (1993), but correspond with the reports of Trus and Wilton (1988) who reported r_{am} of 0.55 for Shorthorn cattle. The negative r_{am} values estimated for WWt and ADG are consistent with those reported by Trus and Wilton (1988) and Swalve (1993), but lower than the estimates of Mostert *et al.* (1998), Rust *et al.* (1998) Robinson (1996a) and Meyer (1993b) reported for WWt.

The off-diagonal components of the correlation matrix in Table 4 show the correlations between the direct genetic effect of one trait and the maternal genetic effect of another trait or *vice versa* (cross-correlation). The correlation estimates between the direct genetic effect of BWt and maternal genetic effect of WWt (Model 3) agreed well with the average literature estimate of -

0.12 (Koots *et al.*, 1994b). The estimate from Model 4 was stronger and negative than this average, but lie within the range of -0.20 to -0.58 estimated by Mostert *et al.* (1998). On the other hand, the correlation between the maternal genetic effect of BWt and the direct genetic effect of WWt was very strong and positive (Model 3 =0.72, Model 4 =0.77) compared to the average value of -0.07 reported by Koots *et al.* (1994b). Likewise, the direct genetic effect of BWt was negatively correlated with the maternal genetic effect of ADG and the maternal genetic effect of BWt was positively correlated with the direct genetic effect of ADG. The reason for this difference is not obvious. The correlation between direct or maternal genetic effects for WWt and maternal or direct genetic effects for ADG were both negative. Selection for direct breeding values of WWt and ADG would thus increase maternal breeding values of BWt, while selection for increased maternal breeding values of WWt and ADG would tend to decrease direct breeding values for BWt.

Conclusion

Models for analysis of genetic parameters of early growth traits need to include maternal effects. Estimates of heritabilities from a simple animal model tend to be larger than in most comparable studies, although large genetic variation in this multibreed herd may also be a reason for fairly high heritabilities. The magnitude of heritability estimates indicated that opportunity exists to improve these traits through selection. Maternal

permanent environmental effects turned out to be more important than maternal genetic effects for weaning weight and average daily gain.

In the future, similar traits of economic importance such as cow efficiency and carcass traits should also be evaluated in a similar way, although such traits are not expected to be as related to maternal attributes as for the preweaning traits investigated in this study. Despite the fact that multitrait animal model analyses are computationally demanding, they are the most appropriate way of estimating (co)variance components and genetic parameters of growth traits.

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