

Model comparisons and genetic and environmental parameter estimates of growth and the Kleiber ratio in Horro sheep

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Abstract

Genetic and environmental parameters were estimated for pre- and post-weaning average daily gain (ADG1, ADG2) and Kleiber ratio (KR1, KR2) using the ASREML program. Twelve models, formed with inclusion or exclusion of the maternal genetic, permanent environmental and common (litter) environmental variance components and the covariance between the direct and maternal additive effect on the basic direct additive genetic model, were used. The same models were applied to birth weight (BWT), weaning weight (WWT) and bi-monthly weights to 12 months of age (WT2 to WT12), and weight at 18 months of age (WT18). Two-trait analyses were done among all traits. Maternal genetic and common environmental components were found to be important for ADG1, KR1 and weights up to six-months of age, while the common environmental component was found to be important for ADG2 and KR2. The maternal permanent environmental component was important for WT2 and WWT. Total heritability estimates for ADG1, ADG2, KR1 and KR2 were 0.13, 0.04, 0.13, and 0.01, respectively. Direct genetic correlations of ADG1 with BWT, WWT and WT6 were 0.01, 0.96 and 0.84 while with KR1 they were -0.40, 0.75 and 0.66, respectively. The relatively higher heritability in weight traits and the presence of positive and high correlations of weight traits with daily gain and Kleiber ratio tend to suggest that it would be more practical to select on the weight traits to improve gain and efficiency.

Keywords: Average daily gain, Kleiber ratio, common environmental effect, genetic parameters

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Introduction

A slow growth rate, resulting in a low market weight of sheep, has been identified to be one of the factors limiting profitability in the highlands of Ethiopia, where about 75% of the country's sheep population is found. (Mukasa-Mugerwa & Lahlou-Kassi, 1995). Genetic improvement can be one of the avenues to improve growth rate. The Kleiber ratio (KR) has been suggested to be a useful indicator of efficiency of growth and an important selection criterion for efficiency of growth (Bergh, 1990; Köster *et al.*, 1994). In a recent study Arthur *et al.* (2001) showed that the KR is highly correlated ($r = -0.81$) with feed conversion efficiency in beef cattle. In addition the possibility also exists to select for weight per age traits in order to improve the marketable weight of sheep. Studies elsewhere (Tosh & Kemp, 1994; Saatci *et al.*, 1999; Maniatis & Pollott, 2002; Van Wyk *et al.*, 2003) indicated that the maternal environmental effects have sizeable contributions to the overall variance. Incorporation of this component in the analytical models will thus contribute to the accuracy of estimates of parameters while exclusion may lead to biased estimates (Van Wyk *et al.*, 1993; Saatci *et al.*, 1999; Satoh *et al.*, 2002). Genetic parameters may vary because of genotype, breed, location or herd. Hence, appropriate parameter estimates for growth traits are important for adequate breeding strategies and for accurate breeding value estimation.

The objectives of this study were to compare different models and estimate genetic and environmental parameters for average daily gain, Kleiber ratio, bi-monthly weights from birth to 12-months, 12-month weight weaning weights and 18 month weights of Horro sheep. The information generated would be useful in designing breed improvement programs in Ethiopia.

Material and Methods

The Horro sheep breed is one of the dominant sheep breeds in Ethiopia and has been adequately described by Galal (1983). On-station performance data on the breed have been collected from 1978 to 1997 at Bako Research Centre, Ethiopia. A detailed description of the environment, flock management and data collection procedures has been reported by Abegaz *et al.* (2002). After preliminary editing for outliers, 4031 lambs born from 3014 parturitions of 904 ewes and 184 sires were used. Further editing for missing or doubtful values with respect to fixed effects and pedigree has resulted in the data described in Table 1. Traits considered were pre- and post-weaning average daily gain (ADG1 & ADG2, respectively) and pre and post-weaning Kleiber ratio (KR1 & KR2, respectively). Bi-monthly weights from birth to one-year of age (BWT, WT2 to WT12), weaning weight (WWT) at about three months of age and eighteen-month weight (WT18) were also considered. The ADG1 and ADG2 were calculated as total gain divided by the number of days in the period while KR1 and KR2 were calculated as a ratio of ADG to metabolic weight at weaning and six months of age, respectively.

Important fixed effects and interactions for all traits were identified from preliminary analysis using the GLM procedure of SAS (1994). Year of birth, sex, type of rearing (type of birth for BWT and WT2) and age at measurement were found to be significant ($P < 0.05$) in all cases. Age of dam was also found to have a significant effect ($P < 0.05$) on pre-weaning gain and KR1 as well as weights to the age of 12 months. Year of birth and sex were combined into a class to account for the interaction after weaning due to animals of different sexes being raised separately. This interaction was found to be important for 12 and 18-month weights.

Table 1 Description of the data used in the study

Trait	N	Mean	s.d.	CV (%)	Range	Age (range)
ADG1 (g/d)	2865	100.4	35.7	35.6	21-230	-
KR1	2864	15.3	2.49	16.3	6.8-22.8	-
ADG2 (g/d)	2245	36.3	27.3	75.1	-42-131	-
KR2	2257	4.4	3.15	71.6	-7.7-13.3	-
BWT (kg)	3958	2.6	0.61	23.8	1.0-4.5	-
WT2 (kg)	2567	9.7	2.83	29.1	4.0-19.0	60 (38-93)
WWT (kg)	2859	12.0	3.47	28.9	5.0-23.0	93 (70-110)
WT4 (kg)	2422	13.1	3.72	28.3	5.0-27.0	120 (90-152)
WT6 (kg)	2269	15.8	4.25	26.9	6.0-35.0	183 (140-220)
WT8 (kg)	1915	17.8	4.85	27.3	6.0-37.0	238 (202-308)
WT10 (kg)	1627	20.1	5.80	28.7	8.0-45.0	294 (258-366)
WT12 (kg)	1469	23.8	6.36	26.8	11.0-45.0	366 (322-408)
WT18 (kg)	1013	27.3	7.08	25.9	12.5-51.0	528 (481-597)

ADG1, ADG2, KR1 and KR2 = pre- and post-weaning daily gain and Kleiber ratio, respectively; BWT = birth weight; WWT = weaning weight; WT2 to WT12 = bi-monthly weights from 2 to 12 months; WT18 = 18 month weight

(Co)variance components were estimated for each trait under an animal model in a univariate analysis using the ASREML program (Gilmour *et al.*, 1999). Twelve different models were used (Table 2). Tests of significance of each random effect were performed using log likelihood ratio tests after including each random effect (excluding residual) to the fixed effects model. An effect was considered significant when its inclusion in the model caused a significant increase in the log likelihood. A Chi-square distribution for $\alpha = 0.05$ and one degree of freedom was used as the critical test statistic (3.841). When -2 times the difference between log likelihoods was greater than the critical value the inclusion of the effect was considered significant. Correlations and cross-correlations between the different components of the different traits were

estimated from bivariate analyses using the appropriate model for each of the traits. In some cases convergence was not possible to achieve in the bivariate analysis and thus a 'reduced' model where one or more random components were removed, was used in the analysis. When differences between log likelihoods were not significant the model with the fewest random effects was chosen. The following univariate animal models (in matrix notation) were fitted:

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

$$y = Xb + Z_1a + Z_2t + e \quad (2)$$

$$y = Xb + Z_1a + Z_2pe + e \quad (3)$$

$$y = Xb + Z_1a + Z_2pe + Z_3te + e \quad (4)$$

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

$$y = Xb + Z_1a + Z_2m + Z_3te + e \quad \text{with cov (a,m) = 0} \quad (6)$$

$$y = Xb + Z_1a + Z_2m + e \quad \text{with cov (a,m) = } A\sigma_{am} \quad (7)$$

$$y = Xb + Z_1a + Z_2m + Z_3te + e \quad \text{with cov (a,m) = } A\sigma_{am} \quad (8)$$

$$y = Xb + Z_1a + Z_2m + Z_3pe + e \quad \text{with cov (a,m) = 0} \quad (9)$$

$$y = Xb + Z_1a + Z_2m + Z_2pe + Z_3te + e \quad \text{with cov (a,m) = 0} \quad (10)$$

$$y = Xb + Z_1a + Z_2m + Z_3pe + e \quad \text{with cov (a,m) = } A\sigma_{am} \quad (11)$$

$$y = Xb + Z_1a + Z_2m + Z_3pe + Z_4te + e \quad \text{with cov (a,m) = } A\sigma_{am} \quad (12)$$

where y was a vector of observations for the different traits, b , a , m , pe and te were vectors of fixed effects, direct and maternal genetic effects, permanent and temporary (litter) environmental effects due to the dam, respectively. Matrices X , Z_1 , Z_2 , Z_3 and Z_4 were the corresponding incidence matrices relating observations to the respective fixed and random effects and e was the vector of residuals. It was assumed that: $V(a) = A\sigma_a^2$; $V(pe) = I\sigma_{pe}^2$; $V(te) = I\sigma_{te}^2$; $V(e) = I\sigma_e^2$, with A being the numerator relationship matrix, I identity matrices of order equal to the number of dams, number of litters and number of records respectively, σ_a^2 , σ_m^2 , σ_{pe}^2 , σ_{te}^2 and σ_e^2 direct and maternal genetic variance, dam permanent environmental variance (half sibs across years), temporary environmental variance (full sibs within year) and environmental (residual) variance respectively.

Results and Discussion

Log likelihood values for the different models on all traits are presented in Table 2. Maternal genetic components were significant ($P < 0.05$) for ADG1 and KR1 and for weights to eight months of age. In the presence of the other components, with the exception of WT2 and WWT, the permanent environmental component was found to have no significant ($P > 0.05$) contribution to ADG1, ADG2, KR1, KR2 and weights to the different ages. Structure of data (i.e. number of records per dam, the proportion of dams with their own record) has been reported to affect the accuracy of partitioning of maternal genetic and environmental effects (Maniatis & Pollott, 2003). In the current study, the data structure was acceptable since most of the dams have their own records and, on average, each dam has had more than three lambing records. The temporary environment was found to be important for ADG1, ADG2, KR1, KR2 and weights to the age of six months. The importance of the temporary environmental effect was highest for BWT and it declined with age, as expected. The covariance between direct and maternal genetic effects was found to be significant ($P < 0.05$) for ADG1 and weights to weaning (BWT, WT2, WWT). In the literature carry-over effect of the maternal genetic effect was shown to persist for longer periods, namely to the age of 18 months (Snyman *et al.*, 1996) and 22 months (Vaez Torshizi *et al.*, 1996) and the permanent environmental effect to the age of 12 months (Matika *et al.*, 2003). Lewis & Beatson (1999) observed that the permanent environmental effect was important for hogget weight, which was taken between 8 and 12 months of age.

Numerous reports have been published on the contribution and importance of the maternal genetic variance, permanent environmental variance and direct-maternal genetic covariance in improving the fit of models for growth performance in sheep (e.g. Van Wyk *et al.*, 1993; Maria *et al.*, 1993; Snyman *et al.*, 1996; Okut *et al.*, 1999; Cloete *et al.*, 2001, Maniatis & Pollott, 2002) and goats (e.g. Van Niekerk *et al.*, 1996).

Due to low rates of multiple births in some sheep breeds and also due to the analytical problem that might arise when maternal genetic, permanent environmental and temporary environmental (litter) effects are fitted simultaneously, there are few reports that considered the importance of the litter variance in model choice. Improved fit of analytical models by the inclusion of a temporary environmental component (fitted with different other components) has been reported for weaning and hogget live weight of New Zealand Coopworth sheep (Lewis & Beatson, 1999) for weights at weaning (about 65 days), 90 and 120 days of crosses involving three breeds (Al-Shorepy & Notter, 1996) for birth and weaning weight of Dormer sheep (Van Wyk *et al.*, 2003) and for 12-week weight of Welsh mountain lambs (Saatci *et al.*, 1999). Schoeman *et al.* (1997) and Hagger (1998) have also reported significant litter effects for birth and weaning weight, ADG and Kleiber ratio of Boer goat and for ADG in the first 30 days of two breeds of sheep, respectively. However, the twinning rate (35%) of sheep reported in the study of Saatci *et al.* (1999) is similar to that in the current study (34%). This implies the temporary environmental effect can have a significant effect even in situations where the incidence of twinning is as low as slightly above 30%.

Genetic and environmental parameter estimates for all traits are presented in Table 3. Estimates of total heritability for ADG1 and KR1 were 0.13 and 0.13. Total heritability (h^2_t) estimates are useful in estimating response for selection based on phenotypic values. For comparison, h^2_t was calculated from studies in the literature that reported direct and maternal variance and covariance. Corresponding estimates for ADG1 ranging from 0.08 to 0.27 in sheep (Van Wyk *et al.*, 1993; Analla *et al.*, 1995; Yazdi *et al.*, 1997; Hagger, 1998; Larsgard & Olesen, 1998; Matika *et al.*, 2003) and goats (Van Niekerk *et al.*, 1996; Schoeman *et al.*, 1997) have been reported. The current estimate falls on the lower end of this range. For KR1 literature estimates for total heritability ranged from 0.09 for Sabi sheep (Matika *et al.*, 2003) to 0.15 for Dormer sheep (Van Wyk *et al.*, 1993) and to 0.16 in the Boer goat (Van Niekerk *et al.*, 1996; Schoeman *et al.*, 1997). These values are consistent with the estimate of 0.13 in this study.

For weights from birth to six months of age, the temporary environmental effect accounted for 11 to 51% of the total variation while the maternal genetic component accounted for 5 to 17% for weight until about 8 months of age (Table 4). The permanent environmental variance component accounted for 7 and 6% of the variation in WT2 and WWT, respectively. From models with varying components fitted simultaneously, proportions of temporary environmental variance ranging from 0.04 to 0.44 were reported for birth weight and weaning weight (Al-Shorepy & Notter, 1996; Larsgrad & Olesen, 1998; Lewis & Beatson, 1999; Nagy *et al.*, 1999; Saatci *et al.*, 1999). Tosh & Kemp (1994) also reported that litter effect accounted for 0.12 to 0.30 of the variance in weights recorded at birth, 50 days and 100 days of age. The estimate of 0.51 in the current study for BWT is higher than estimates in the literature. This may be the result of rounding of birth weights to the nearest quarter kilogram, a procedure followed in the recording of the birth weights. Usually twin born lambs have birth weights close to each other, which become identical when rounded. According to log likelihoods for BWT the permanent environmental effect should not be included in the model. The inclusion or exclusion (Model 8 vs. 12) of this effect was, however, marginal. Therefore, the magnitude of this effect (0.51) should be interpreted with caution since it could be biased.

Estimates of total heritability for BWT, WWT, WT6 and WT12 were 0.14, 0.12, 0.21 and 0.33, respectively. These values are slightly lower for BWT and WWT and higher for WT12 than estimates reported from the same data set fitting other models (model 4 vs. 7 current) by Abegaz *et al.* (2002). Exclusion of important components (in this case litter) obviously has the effect of inflating the remaining parameter estimates. The difference in the heritability estimate of WT12 is the result of difference in the data edit criteria and in the fixed part of the model used in the previous and the current study. For bi-monthly weights from two to 10 months and for WT18, heritability estimates were 0.06, 0.21, 0.21, 0.21, 0.29 and 0.33, respectively. For weight at 18 months of age, Lee *et al.* (2000) reported a direct heritability of 0.43 from a simple animal model, while from a sire model Groenewald *et al.* (1999) have estimated a heritability of 0.34 for weight of Merino sheep recorded between 15 and 18 months of age. The latter value is close to current estimates. The heritability reaches a maximum at the ages of 10 to 12 months and these traits may be used for selection to improve growth given favourable relationships with the other economically important traits.

Genetic and phenotypic correlations and cross-correlations among ADG1, KR1, ADG2, KR2, BWT, WWT, WT6, WT12 and WT18 are presented in Tables 4 and 5. Phenotypic correlations of ADG1 with KR1,

Table 2 Log likelihood values for pre- and post-weaning daily gain (ADG1 & ADG2), Kleiber ratio (KR1 & KR2), birth weight (BWT), weaning weight (WWT) and bi-monthly weights from two months (WT2) to 12 months (WT12) and 18-months weight (WT18) with values from the most appropriate model^{a)} (in bold)

Model	Trait												
	ADG1	KR1	ADG2	KR2	BWT	WT2	WWT	WT4	WT6	WT8	WT10	WT12	WT18
1	-10832.2	-3543.09	-8234.28	-3531.6	571.49	-3190.71	-4213.04	-3668.57	-3470.94	-3323.76	-2972.83	-2778.24	-1895.13
2	-10823.9	-3500.00	-8229.97	-3526.79	749.07	-3180.00	-4204.76	-3658.81	-3731.59	-3322.64	-2972.52	-2778.01	-1895.13
3	-10808.7	-3529.27	-8234.26	-3531.38	603.52	-3171.26	-4183.91	-3661.20	-3738.64	-3322.31	-2972.85	-2777.23	-1894.91
4	-10806.8	-3521.41	-8229.97	-3526.79	757.39	-3165.98	-4181.00	-3654.72	-3730.65	-3321.73	-2972.52	-2777.20	-1894.91
5	-10806.5	-3528.26	-8233.87	-3531.36	598.56	-3172.32	-4182.61	-3656.12	-3733.61	-3319.79	-2972.82	-2776.75	-1895.06
6	-10802.2	-3518.78	-8228.78	-3526.73	758.09	-3166.12	-4178.91	-3649.39	-3726.48	-3319.32	-2972.52	-2776.73	-1895.06
7	-10804.8	-3527.73	-8233.60	-3531.06	604.18	-3170.11	-4180.19	-3655.79	-3733.61	-3319.66	-2971.73	-2774.89	-1894.91
8	-10800.3	-3518.12	-8229.74	-3526.71	761.66	-3163.91	-4176.46	-3648.99	-3726.46	-3319.14	-2971.51	-2774.88	-1894.91
9	-10804.4	-3526.30	-8234.06	-3531.32	606.50	-3168.86	-4179.49	-3656.12	-3734.37	-3319.79	-2972.82	-2776.69	-1894.91
10	-10800.8	-3517.99	-8229.78	-3526.73	759.61	-3163.61	-4176.47	-3649.39	-3727.61	-3319.32	-2972.52	-2776.68	-1894.91
11	-10802.9	-3525.87	-8233.60	-3531.04	611.98	-3166.89	-4177.55	-3655.79	-3733.61	-3319.66	-2971.73	-2774.77	-1894.73 ¹⁾
12	-10799.2	-3517.39	-8229.74	-3526.71	763.33	-3161.57	-4174.44	-3648.99	-3726.46	-3319.14	-2971.51	-2774.77	-1894.73 ¹⁾

^{a)}P < 0.05 was used to identify the best model

Table 3 Parameter estimates for pre- and post-weaning average daily gain and Kleiber ratio, bi-monthly body weights to 12 months, weaning weight and 18 month weight

Trait	σ^2_p	h^2_a	h^2_m	r_{am}	te^2	pe^2	h^2_t
ADG1	771.1	0.15±0.048	0.20±0.040	-0.45±0.160	0.13±0.039		0.13±0.038
KR1	4.28	0.09±0.036	0.08±0.022		0.19±0.040		0.13±0.034
ADG2	596.8	0.04±0.026			0.22±0.051		0.04±0.026
KR2	7.86	0.01±0.022			0.20±0.053		0.01±0.022
BWT	0.265	0.20±0.048	0.10±0.029	-0.53±0.133	0.51±0.024	-	0.14±0.033
WT2	4.282	0.10±0.047	0.11±0.041	-0.53±0.200	0.17±0.043	0.07±0.033	0.06±0.035
WWT	6.81	0.16±0.045	0.15±0.049	-0.47±0.167	0.11±0.039	0.06±0.031	0.12±0.038
WT4	7.50	0.16±0.045	0.09±0.025	-	0.16±0.041	-	0.21±0.041
WT6	9.78	0.18±0.046	0.07±0.024	-	0.17±0.044	-	0.21±0.042
WT8	11.55	0.18±0.049	0.06±0.026	-	-	-	0.21±0.044
WT10	13.98	0.29±0.053	-	-	-	-	0.29±0.053
WT12	18.49	0.33±0.055	-	-	-	-	0.33±0.055
WT18	20.41	0.33±0.069	-	-	-	-	0.33±0.069

ADG1 and ADG2 = pre- and post-weaning daily gain, respectively; KR = Kleiber ratio; BWT = birth weight; WWT = weaning weight; WT2 – WT18 = bi-monthly weights from two months and 18 months weight; σ^2_p = Phenotypic variance, direct heritability (h^2_a); maternal heritability (h^2_m); direct-maternal genetic correlation (r_{am}); ratios of temporary (te^2) and permanent (pe^2) environmental variance and total heritability (h^2_t); Total heritability = $(\sigma^2_a + 0.5\sigma^2_m + 1.5\sigma_{am}) / \sigma^2_p$ (Willham, 1972)

ADG2, and KR2 were 0.98, -0.11 and -0.27, while genetic correlations were 0.96, 0.63 and 0.89, in the respective order. It appears that lambs with higher gain in the pre-weaning period gain less and are also less efficient during the post-weaning period on the phenotypic level and *vice versa*. Positive genetic correlations between ADG1 and ADG2 in the presence of negative phenotypic correlations might have arisen as a result of compensatory growth mediated through environmental effects in lambs that were gaining at lower rates during the pre-weaning period. Similar negative phenotypic correlations between pre- and post-weaning ADG have been reported for Muzaffarnagri sheep (Sinha & Singh, 1997) and for Baluchi sheep (Yazdi *et al.*, 1997) while Maria *et al.* (1993) have reported high positive phenotypic correlations for Romanov sheep. With respect to genetic correlations, Maria *et al.* (1993) and Yazdi *et al.* (1997) have reported negative genetic correlations between pre- and post-weaning ADG. Phenotypic and genetic correlations between ADG1 and KR1 were reported to be 0.93 and 0.94 in Dorner sheep by Van Wyk *et al.* (1993). Van Niekerk *et al.* (1996) estimated a corresponding genetic correlation of 0.97 on Boer goats using a sire model. These estimates are in accordance with the values obtained in the current study (0.98 phenotypic and 0.96 genetic).

Except for maternal additive correlations with ADG1 and KR1, all correlations and cross correlations between BWT and ADG1, KR1, ADG2 and KR2 were low and in some cases negative. This indicates that maternal genetic (additive) effects, which favour the growth of the foetus, could also have some favourable effect on postnatal growth and efficiency. The absence of any sizeable direct additive correlation between ADG1 and BWT (and medium maternal genetic correlations) indicates that these traits are not antagonistic to each other. Bromley *et al.* (2000) have reported direct correlations ranging from 0.18 to 0.57, maternal correlations ranging from -0.03 to 0.40, and cross correlations of -0.12 to 0.21 between BWT and ADG in four breeds of sheep. The maternal genetic correlation estimate of 0.68, though slightly higher, agrees with the estimate of Bromley *et al.* (2000).

Cross correlations between the direct and maternal additive effects of ADG1 with WWT, were negative (-0.36 to -0.39), while the phenotypic, direct additive, maternal additive and residual correlations were positive and high (0.72 to 1.00). Similarly, Analla *et al.* (1995) have reported negative cross correlations for all direct and maternal variances of WWT, ADG, and weight at 90 days of age. High correlations between pre-weaning daily gain and weaning and subsequent weights are expected, as this is governed by a part-whole relationship.

Table 4 Estimates of phenotypic (r_{p12}), direct genetic (r_{a12}), maternal genetic (r_{m12}), and residual (r_{e12}) correlations and direct-maternal (r_{a1m2}), maternal direct (r_{a2m1}) genetic cross correlations among pre and post-weaning gain and Kleiber ratio and with weight at birth, weaning, six months, 12-months and 18-months of age

Trait ^{a)}		KR1	ADG2	KR2	BWT	WWT	WT6	WT12	WT18
ADG1	r_{p12}	0.98±0.003	-0.11±0.023	-0.27±0.021	0.09±0.03	0.72±0.072	0.61±0.025	0.53±0.026	0.50±0.031
	r_{a12}	0.96±0.016	0.63±0.333	0.89±0.466	0.04±0.21	0.96±0.016	0.92±0.093	0.79±0.12	0.48±0.164
	r_{e12}	0.95±0.004	-0.18±0.052	-0.39±0.046	0.06±0.06	1.00±0.002	0.64±0.019	0.42±0.039	0.42±0.049
	r_{m12}	0.99±0.014			0.68±0.15	1.00±0.004	0.92±0.067	-	
	r_{a1m2}	-0.40±0.19			-	-0.39±0.164	0.16±0.103	0.39±0.141	0.48±0.136
	r_{a2m1}	-0.41±0.22	0.46±0.250		-	-0.36±0.170	-0.03±0.151	-	-
KR1	r_{p12}		-0.11±0.024	-0.28±0.022	-	0.75±0.032	0.48±0.054	0.44±0.027	0.45±0.032
	r_{a12}		0.59±0.364	0.33±0.540	-	0.74±0.096	0.66±0.155	0.56±0.168	0.55±0.179
	r_{e12}		-0.18±0.052	-0.37±0.046	-	0.87±0.009	0.52±0.027	0.40±0.045	0.39±0.051
	r_{m12}				0.56±0.24	0.89±0.059	0.81±0.112	-	-
	r_{a1m2}				-	-0.19±0.151	-0.10±0.202	0.40±0.180	0.61±0.154
	r_{a2m1}		0.44±0.272	0.69±0.447	0.10±0.25	0.032±0.12	0.05±0.304	-	-
ADG2	r_{p12}			0.96±0.008 ^{b)}	0.02±0.02	-0.12±0.023	0.61±0.016	0.26±0.024	0.23±0.031 ^{b)}
	r_{a12}			0.99±0.006 ^{b)}	-	0.54±0.365	0.90±0.160	0.99±0.00	1.00±0.233 ^{b)}
	r_{e12}			0.96±0.003 ^{b)}	0.04±0.06	-0.20±0.050	0.58±0.036	0.20±0.034	0.17±0.050 ^{b)}
	r_{a2m1}			-	0.09±0.31	0.51±0.277	0.41±0.234	-	-
	r_{p12}				-	-0.25±0.024	0.43±0.018	0.16±0.026 ^{b)}	-0.19±0.027
KR2	r_{a12}				-	0.47±0.52	0.91±0.514	-	0.82±0.988
	r_{e12}				-	-0.37±0.027	0.44±0.026	0.11±0.032 ^{b)}	-0.23±0.034
	r_{a2m1}				-	0.60±0.401	-	-	-

^{a)} = First row trait 1, first column trait two; ADG1 = pre-weaning daily gain; KR1 = pre-weaning Kleiber ratio; ADG2 = post-weaning gain; KR2 = post-weaning Kleiber ratio; BWT = birth weight; WWT = weaning weight; WT6 = six month weight; WT12 = 12-month weight; WT18 = 18-month weight;

^{b)} = A 'reduced' model (one or more random components removed) was used due to lack of convergence when the best model for either one or both of the traits was used in the bivariate analysis

Table 5 Estimates of phenotypic (r_{p12}), direct genetic (r_{a12}), maternal genetic (r_{m12}) and residual (r_{e12}) correlation estimates and direct-maternal (r_{a1m2}), maternal direct (r_{a2m1}), genetic cross correlation estimates between birth, weaning, six month, 12-month and 18-month weights

Trait1	BWT	BWT	BWT	BWT	WWT	WWT	WWT	WT6	WT6	WT12
Trait2	WWT	WT6	WT12	WT18	WT6	WT12	WT18	WT12	WT18	WT18
$r_{p12}^{a)}$	0.27±0.035	0.23±0.034	0.16±0.029	0.14±0.034	0.60±0.034	0.54±0.026	0.50±0.031	0.61±0.02	0.55±0.028	0.69±0.018
	0.25±0.021	0.21±0.024	0.12±0.029		0.73±0.011	0.51±0.021		0.57±0.019		
$r_{a12}^{a)}$	0.29±0.196	0.27±0.196	0.28±0.154	0.05±0.186	0.92±0.101	0.76±0.116	0.48±0.139	0.83±0.093	0.77±0.120	0.99±0.038
	0.45±0.093	0.33±0.106	0.31±0.113		0.98±0.023	0.84±0.065		0.87±0.062		
r_{e12}	0.18±0.062	0.22±0.068	0.13±0.069	0.16±0.083	0.69±0.016	0.43±0.038	0.41±0.050	0.54±0.038	0.43±0.049	0.56±0.036
r_{m12}	0.77±0.142	0.73±0.023	-		0.96±0.056					
r_{a1m2}	-0.29±0.187	-0.31±0.279	-		-0.39±0.198					
r_{a2m1}	-0.11±0.212	0.01±0.205	0.16±0.16	0.35±0.17	0.04±0.118	0.37±0.137	0.53±0.139	0.44±0.157	0.55±0.142	

BWT = birth weight; WWT = weaning weight; WT6 = six month weight; WT12 = 12 month weight

^{a)} = Estimates in the second line of the row are from a previous study (Abegaz *et al.*, 2002) on a direct additive model for both traits

All direct genetic correlations between the weights were lower than values reported from the same data set using only direct animal models for all traits (Abegaz *et al.*, 2002). Similar overestimation of the direct genetic covariance when models do not include maternal effects, has been reported by Analla *et al.* (1995) for sheep and by Meyer (1994) for beef cattle. Cross correlations between direct and maternal effects of the weight traits were low to medium and in some cases negative.

Conclusions

Genetic variation in early growth traits in the Horro sheep is sufficient to warrant inclusion in the breeding objectives. A number of findings from the current and a previous study (Abegaz *et al.*, 2002) indicate that weight at about one year of age is the most important trait to consider in improving productivity in Horro sheep. In Ethiopia the great majority of sheep for slaughter are unfinished milk tooth lambs weighing 10 to 20 kg (Galal *et al.*, 1979; Kassahun, 2000). This weight is achieved from about the age of six months to one year of age. The existence of high correlations between body weight at one year of age and earlier ages allows earlier weights to respond to improvement protocols based on 12-month weight, and it also permits some initial culling on performance at an earlier age. As reported in numerous studies in other breeds, the results of this study confirm that for accurate parameter estimation of growth performance and efficiency during the early life of Horro sheep, models should consider the maternal genetic, permanent and temporary environmental components.

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