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Estimates of Maternal Effect and (co)Variance Components for BodyWeight at Different Ages by Animal Model in Chokla Sheep

Garima Choudhary[1], Urmila Pannu[1], H.K. Narula[2], Gopal Gowane[3],
Ashish Chopra[4], N.K. Poonia[5], Manju Nehara[1]

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ABSTRACT

Background: For this study, information was gathered on 6785 Chokla sheep at the Central Sheep and Wool Research Institute in Bikaner, Rajasthan, India and documented between 1974 and 2020.

Methods: (Co)variance components and genetic parameters of weight at birth (BW), weaning (WW), 6, 9 and 12 months of age (6W,9W and YW, respectively) of Chokla sheep, were estimated by average algorithm restricted maximum likelihood (AIREML), fitting six different animal models with various combinations of direct and maternal effects.

Result: The direct heritability estimates increased from birth to twelve months of age and values for all the body weight traits except birth weight (0.170) were moderate (0.30-0.50). The maternal influence diminished as age increases and maternal genetic effect (m^2) was found to be important and sizeable at weaning stage (0.181). Maternal permanent environmental variance was found to influence the early body weight traits. Negative and high estimate of covariance between direct and maternal effects, resulted in highly inflated values of additive heritability. In this condition, it is more useful to use the total heritability (h^2_t) for evaluation of the response for selection based on phenotypic values to prevent the use of biased estimates of additive heritability. Genetic and phenotypic correlations among body weights at different ages were positive and ranged from medium to high.

Key words: Chokla, (Co)variance components, Genetic correlation, Genetic parameters, Maternal effect, Phenotypic correlation.

INTRODUCTION

Small ruminants serve the mankind in multiple ways of providing protein rich food, supplementing farmers' income, facilitating rural employment and improving soil fertility. So these animals play an important role for the socio-economic upliftment of small, marginal farmers and landless labourers in our country. Growth is a merit of interest in livestock animals. Information about growth model parameters is very serviceable for selection polices in Madras Red sheep (Ganesan *et al.* 2015). A number of non-genetic factors affect these growth traits and directly obscure recognition of the genetic potential. Improvement in production, without affecting adaptability can be brought about only by genetic improvement through selection and breeding. Formulation of breeding programmes require accurate values of genetic parameters, for which precise estimates of (co)variance components, obtained after adjustment for various non-genetic factors are a pre-requisite.

An animal model like DFREML takes into accounts all relationship in the pedigree and is therefore expected to provide estimates of genetic parameters with higher precision. DFREML estimates of covariance components through a derivate free methods while, the AI algorithm (AIREML) is an iterative method which needs initial values of variance components. In mammals, including most livestock species, because there are long periods of maternal dependence, the early growth traits are not controlled only by direct additive genetic effects but also by maternal effects (Gowane *et al.,* 2015 and Aguirre *et al.,* 2016). Maternal effects have been defined as any influence

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[1]Department of Animal Genetics and Breeding, College of Veterinary and Animal Science, Rajasthan University of Veterinary and Animal Sciences, Bikaner-334 001, Rajasthan, India.

[2]ICAR-National Bureau of Animal Genetic Resources, Karnal-132 001, Haryana, India.

[3]ICAR-National Dairy Research Institute, Karnal-132 001, Haryana, India.

[4]Central Sheep and Wool Research Institute-Arid Region Campus, Beechwal, Bikaner-334 001, Rajasthan, India.

[5]Department of Livestock Production Management, College of Veterinary and Animal Science, Rajasthan University of Veterinary and Animal Sciences, Bikaner-334 001, Rajasthan, India.

Corresponding Author: Garima Choudhary, Department of Animal Genetics and Breeding, College of Veterinary and Animal Science, Rajasthan University of Veterinary and Animal Sciences, Bikaner-334 001, Rajasthan, India. Email: drgarima2691@gmail.com

orcid id: https://orcid.org/0000-0002-4001-9625.

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from a dam on its offspring, excluding the effects of directly transmitted genes that affect performance of the offspring. Maternal environmental effect can be partitioned in to permanent and common sectors. However, the later has been ignored in most genetic studies on growth traits. It was observed by various authors that when maternal genetic effects are important and not considered in the statistical model, heritability estimates are biased upwards and the realised efficiency of selection is reduced when compared with the expected. Thus, both direct and maternal components must be considered in order to achieve optimum genetic progress especially in growth traits. Recently many studies have attributed most of the variation in lamb weights to maternal effects (Prince *et al.,* 2010; Abbasi *et al.,* 2012; Gowane *et al.,* 2015; Aguirre *et al.,* 2016; Radwan *et al.,* 2018; Latifi and Mohammadi, 2018 and Mahala *et al.,* 2020).

Hence, present study was undertaken to estimate various (co)variance components and genetic parameters for body weight at different ages.

MATERIALS AND METHODS

Data and management at research station

Data and pedigree information on 6785 Chokla sheep belonging 459 sires and 2102 dams maintained at the Central Sheep and wool Research institute, Arid Region Campus Beechwal, Bikaner were collected over a period of 47 years (1974 to 2020). This institute is geographically located at an altitude of 234.84 meters above mean sea level on 28°3′N Latitude and 37°5′E Longitude.Chokla sheep were reared under semi intensive system of management and all animals grazed during the day (7 to 8 h) on natural pasture with supplementation depending upon the status and age category of the animals and were penned at night. At birth each lamb was identified and date of birth, sex, type of birth and weight were recorded. Lambs were normally weaned at three months of age. Dry fodder supplementation, 300 g of concentrate mixture was also provided during the post-weaning period. The main breeding season generally commenced towards the mid of August and continued for 2-3 oestrus cycles (up to beginning of November). However, a minor season of mating was also executed in the month of March-April to augment the more lambing per year. The prophylactic measures such as vaccination, deworming, dipping and hygienic measures like dusting, spraying, disinfection of sheds, watering channels, feeding troughs and protection of lambs against inclement weather conditions and prophylactic antibiotic treatment of lambs were implemented.

Classifications of data

The data were classified according to period, season and sex of lamb. These data were classified into eleven different periods of 4 years interval each except period P1, P2 and P11to provide unbiased allocation of observations in each period or to avoid the unequal distribution in each period.These periods were P1 (1974-1978), P2 (1979-1983), P3 (1984-1987), P4 (1988-1991), P5 (1992-1995), P6 (1996-1999), P7(2000-2003), P8(2004-2007), P9(2008-2011), P10(2012-2015) and P11 (2016-2020). According to season of lambing data were classified into two season *viz*. spring (January to June) and autumn (July to December). Data were classified according to sex into male and female group.

Statistical analyses of data

The data were analysed to examine the effects of period, season, sex and ewe weight at lambing using least-squares analysis of variance with software SPSS VERSION 26.0 (2005). The model was as follows:

$$Y_{ijklm} = \mu + S_i + A_j + B_k + C_l + b\,(DW_{ijkl} - DW) + e_{ijklm}$$

Where,

Y_{ijklm} = Growth performance record of the mth progeny of ith sire born in jth period, kth season belonging to lth sex.

ì = Overall mean.

S_i = Random effect of ith sire.

A_j = Fixed effect of jth period of birth (j = 1, 2, 3 ...11).

B_k = fixed effect of kth season of birth (k = 1, 2).

C_l = Fixed effect of lth sex of lamb (l = 1, 2).

DW_{ijkl} = Dam’s weight at lambing.

DW = Mean dam’s weight at lambing.

$b\,(DW_{ijkl} - DW)$ = The regression of the corresponding trait on dam’s weight at lambing.

e_{ijklm} = Residual random error under standard assumption which make the analysis valid, *i.e*. NID $(0,\sigma^2)$.

The differences between the least-squares means for subclass under a particular effect were tested by Duncan’s multiple range test (Kramer, 1957).

(Co)Variance components and corresponding genetic parameters for the studied traits were estimated by average information Restricted Maximum Likelihood (AIREML)using the WOMBAT programme (Meyer, 2007) by fitting an animal model throughout.

Only significant effects ($P \leq 0.05$) were included in the models which were subsequently used for the estimation of genetic parameters.

The following animal models by ignoring or including various combinations of maternal genetic and permanent environmental effects were fitted to estimate genetic parameters for each trait:

$Y = Xb + Z_1a + \varepsilon$ Model 1

$Y = Xb + Z_1a + Z_2m + \varepsilon$ with Cov (a,m) = 0 Model 2

$Y = Xb + Z_1a + Z_2m + \varepsilon$ Cov (a,m) = As_{am} Model 3

$Y = Xb + Z_1a + W_c + \varepsilon$ Model 4

$Y = Xb + Z_1a + Z_2m + Wc + \varepsilon$ with Cov (a,m) = 0 Model 5

$Y = Xb + Z_1a + Z_2m + Wc + \varepsilon$ with Cov (a,m) = $A\sigma_{am}$ Model 6

Where,

$Y = N \times 1$ vector of record

b = Fixed effects in the model with association matrix X.

a = Vector of direct genetic effect with the association matrix Z_1.

c = Vector of permanent maternal environmental effect with the association matrix W.

m = Vector of maternal genetic effects with the association matrix Z_2.

e = Vector of residual (temporary environmental) effect.

X, Z_1, Z_2, and W = Incidence matrices that relate these effects to the records such as for b, a, m and c, respectively.

Cov (a,m) indicates covariance between direct and maternal additive genetic effects.

Generally, the (co)variance structure for studied traits was as follows:

$$\text{Var}\begin{pmatrix} a \\ m \\ C \\ e \end{pmatrix} = \begin{pmatrix} A\sigma_a^2 & A\sigma_{am} & 0 & 0 \\ A\sigma_{am} & A\sigma_m^2 & 0 & 0 \\ 0 & 0 & I_d\sigma_c^2 & 0 \\ 0 & 0 & 0 & I_n\sigma_e^2 \end{pmatrix}$$

Additive direct and maternal genetic effects were assumed to be normally distributed with mean 0 and variance $A\sigma_a^2$ and $A\sigma_m^2$, respectively, where A is the additive numerator relationship matrix and σ_a^2 and σ_m^2 are direct additive genetic and maternal additive genetic variances, respectively. σ_{am} is the covariance between additive direct and maternal genetic effect. Permanent environmental effects of the dam and residual effects were assumed to be normally distributed with mean 0 and variances $I_d\sigma_c^2$ and $I_n\sigma_e^2$, respectively, where I_d and I_n are identity matrices with orders equal to the number of dams and individual records, respectively and σ_c^2 and σ_e^2 are maternal permanent environment and residual variances, respectively.

Assumptions for variance (V) and covariance (Cov) matrices involving random effects were:

$$V(a) = A\sigma_a^2$$
$$V(m) = A\sigma_m^2$$
$$V(c) = I_d\sigma_c^2$$
$$V(e) = I_n\sigma_e^2$$

$$\text{Cov}(a,m) = A\sigma_{am}$$

The total heritability (h^2_t), was calculated using the following formula:

$$h^2_t = (\sigma^2_a + 0.5\,\sigma^2_m + 1.5\sigma_{am}) / \sigma^2_p; \text{ (Willham, 1972)}$$
$$\sigma^2_p = \sigma^2_a + \sigma^2_m + \sigma^2_c + \sigma^2_e$$

Heritability estimates of additive direct (h^2), additive maternal (m^2) and permanent environmental effects (c^2) were calculated as ratios of estimates of additive direct (σ^2a), additive maternal (σ^2m) and permanent environment maternal (σ^2c) variance to total phenotypic variance (σ^2p), respectively.

$$h^2 = \sigma^2_a / \sigma^2 p$$
$$m^2 = \sigma^2_m / \sigma^2 p$$
$$c^2 = \sigma^2_c / \sigma^2 p$$

The direct-maternal correlation (ram) was calculated in the following manner:

$$r_{am} = \sigma_{am} / \sqrt{\sigma^2_{a*}\,\sigma^2_m}$$

Maternal across year repeatability for ewe performance was calculated for all the traits as follows:

$$t_m = (¼)\, h^2 + m^2 + c^2 + r_{am} \sqrt{m^2}\sqrt{h^2}\,; \quad \text{(Al-Shorepy, 2001)}$$

Goodness of fit for the models was examined using likelihood based criteria as:

$$AIC = -2\text{Log } L_i + 2p_i \text{ (Akaike 1983)}$$

Where,

log L_i = Maximised log likelihood of model i at convergence.

p_i = Number of parameters obtained from each model; the model with the lowest AIC was chosen as the best approximating model.

Bivariate animal model analysis was carried out in order to estimate genetic and phenotypic correlations between the traits based on the most appropriate single-animal models.

RESULTS AND DISCUSSION

Genetic parameters are important because of the significant information available from ewes and their progeny, allowing for the proper partitioning of genetic variance. Descriptive statistics as estimated by the animal model was summarized for body weights at different ages in Table 1. In contrast to the current findings, Dangi and Poonia (2006) calculated means of WT3 and WT6 being 10.36±0.21 and 13.41±0.27 kg, respectively in crossbred sheep to be lower than those obtained in this paper. Mallick *et al.* (2017) calculated the overall least squares means for weights to be 3.28±0.02, 19.08±0.23 and 25.00±0.35 kg for BW, WT3 and WT6, respectively which higher to current means. They also concluded that genetic parameters estimated of WT6 indicated the possibility for using this trait as a selection criterion to improve body weight in Bharat Merino lambs.

The effect of period of lambing and sex of lamb was found highly significant ($P<0.01$) on all the studied traits. The effect of season of lambing was reported highly significant ($P\leq 0.01$) on all body weights except nine-month body weight. The regression of these traits on weight of ewe at lambing was significant.

(Co) variance components and genetic parameter estimates

One of the fundamental objectives of genetic evaluation exercises is to partition the genetic variance in direct and maternal effects, where applicable. The findings of the present study confirmed the importance of implementing the correct model for estimation of (co)variance components and genetic parameters for growth traits of Chokla sheep. (Co)variance components and genetic parameters estimated by most appropriate model in univariate analysis by WOMBAT for various growth traits of Chokla sheep are summarized in Table 2.

Table 1: Descriptive statistics and data structure for body weights in Chokla sheep.

Trait	BW	WW	6W	9W	YW
No. of records	6769	5683	4911	4297	3689
No. of animals in pedigree	7207	6101	5291	4695	4083
Sires with records and progeny in data	394	374	348	339	318
Dams with records and progeny in data	1716	1561	1475	1368	1269
Animals with known paternal grand sire with progeny	5546	4827	4211	3772	3299
Animals with known paternal grand dam with progeny	5571	4837	4176	3716	3250
Animals with known maternal grand sire with progeny	5705	4916	4272	3794	3293
Animals with known maternal grand dam with progeny	5799	4987	4327	3829	3298
No. of animals without offspring	4659	3741	3079	2580	2092
No. of animals with offspring	2350	2211	2088	1999	1876
Mean (kg)	2.88	13.64	19.32	21.30	24.36
Standard error	0.008	.051	.083	.092	.099
Standard deviation	0.594	3.541	5.070	5.778	5.855
CV%	20.62	25.96	26.24	27.12	24.03
Skewness	-0.20	-0.10	-0.13	0.22	0.06
Non genetic factors					
Period of lambing	**	**	**	**	**
Season of lambing	**	**	**	NS	**
Sex of lamb	**	**	**	**	**
Ewe's weight at lambing	**	**	**	**	**

** - Highly significant ($P\leq 0.01$) ; * - Significant ($P\leq 0.05$); NS- non significant.

The results presented (Table 2) shows an incremental increase in (co)variance component and heritability values for the body weight traits according to age of the animal. This trend was similar, but not of the same magnitude, as that reported by Mohammadi *et al.* (2015), Gowane *et al.* (2015). Gowane *et al.* (2015) found that in Malpura sheep the h^2_a for weight at 90, 180, and 270 days was 0.40, 0.50, and 0.37, respectively and studies reported a negative direct-maternal correlation.

In most studies on growth traits, it has been frequently reported that direct heritability for body weights have a tendency to increase with age (Eskandarinasab *et al.*, 2010). The h^2 values for all the body weight traits except BW were moderate (0.3-0.5). The moderate heritability estimates for growth traits in this study indicates that modest rates of genetic progress may be possible for these traits from selection under the prevailing management system. The estimates for BW were low (0.17). The maximum h^2 estimates were obtained for 9W and YW, with values of 0.510 and 0.515, respectively. The heritability of birth weight (0.173) was in accordance with findings of Gowane*et al.* (2010) as 0.19± 0.04 in Malpura sheep. The direct additive heritability estimates for weaning weight (0.392) and for 6W (0.471) were in close agreement with estimate obtained by Gowane*et al.* (2015) as 0.40±0.06 and 0.50±0.05, for WW and 6W, respectively in Malpura sheep. The value of 9W was found in close agreement with the findings of Aguirre *et al.* (2016) as 0.49 ± 0.06 in Santa Ines and Mahala *et al.* (2020) as 0.50±0.05 in Aviklain sheep. Similarly, Manoj *et al.* (2014) estimated heritability coefficients and their standard errors at different ages of Sahiwal heifers to be 0.13 ± 0.06 and 0.15 ± 0.09 for BW and WT6, respectively. Also, they documented that BW was significant for body weight trait selection in this breed.

The maternal genetic effect (m^2) was found to be important and sizeable at weaning stage (Table 2). In these data, the maternal influence diminished as age increases, but modest genetic progress appears possible for all pre-weaning growth traits analyzed for the Chokla sheep. Maternal genetic effects contributed only 2.4% of the total phenotypic variance from birth to 30 days of age and this effect diminished further with increasing age. These results indicated as lambs grow up, the influence of maternal genetic effects on their growth decreases. The maternal heritability estimated from model 6 for BW and WW and model 3 for remaining different body weight traits show a decreasing trend with advancement in age. The maternal effect is particularly important for early growth traits in sheep as it is influential during pregnancy and lactation, but its importance decreases during the post-weaning stages (Gholizadeh and Ghafouri-Kesbi, 2015). The low maternal effect on pre-weaning growth indicates that the maternal effect would have less effect on selection response for these traits. When maternal effects are of high importance, total heritability values are more efficient than direct heritabilities for estimation of selection response based on phenotypic values.

The permanent environmental effect (c^2) of the dam on birth weight is mainly determined by uterine capacity, feeding level especially at late gestation. Maternal permanent environmental variance was found to influence the early body weight traits of BW and WW and estimates of environmental effects (c^2) for these traits were 0.121 and 0.028, respectively.

Table 2: Estimated genetic parameters and (co)variance components from the best model for each trait.

Traits	Model	Genetic parameters						(co)variance components					
		h^2	m^2	c^2	r_{am}	h_t^2	t_m	σ^2_a	σ^2_m	σ^2_c	σ^2_e	σ^2_p	σ_{am}
BW	6	0.173±0.031	0.168±0.031	0.121±0.019	-0.725±0.068	0.071	0.208	0.041	0.040	0.029	0.159	0.240	-0.029
WW	6	0.392±0.048	0.181±0.029	0.028±0.015	-0.915±0.033	0.118	0.063	2.905	1.343	0.209	4.76	7.418	-1.807
6W	3	0.471±0.045	0.130±0.023	-	-0.923±0.032	0.193	0.020	6.629	1.825	-	8.821	14.06	-3.211
9W	3	0.510±0.048	0.140±0.025	-	-0.914±0.032	0.213	0.023	6.791	1.863	-	7.907	13.310	-3.251
YW	3	0.515±0.052	0.170±0.029	-	-0.928±0.032	0.188	0.024	6.732	2.218	-	7.702	13.066	-3.587

σ^2_a, σ^2_m, σ^2_c, σ^2_e and σ^2_p are additive genetic, maternal additive genetic, maternal permanent environmental, residual variance and phenotypic variance, respectively; h^2 is heritability; C^2 is σ^2_c /σ^2_p; m^2 maternal heritability is σ^2_m /σ^2_p; σ_{am} – direct-maternal genetic covariance; r_{am} – direct- maternal genetic correlation; t_m is maternal across year repeatability for ewe performance; h^2_t is total heritability.

Addition of covariance between direct and maternal effects in model 3 and model 6 has shown negative and high estimate of r_{am}, which resulted in highly inflated values of heritability and maternal effect in these models. It might be due to some hidden mechanism underlying phenotypic relation, which restricts genetic covariance at higher negative magnitude (Prince *et al.*, 2010). To prevent the use of biased estimates of additive direct heritability especially when maternal effects are important it is more useful to use the total heritability (h^2_t) for evaluation of the response for selection based on phenotypic values. Total heritability estimated for BW, WW, 6W, 9W and YW was 0.071, 0.118, 0.193, 0.213, 0.188, respectively.

Reason behind high and negative r_{am} was found by various researchers (Tosh and Kemp 1994; Roff, 2002; Robinson 1996; Berwegeret *al.* 1999 and Notter and Hough, 1997). Antagonism between the effects of an individual's genes for growth and those of its dam for a maternal contribution may be due to natural selection for an intermediate optimum (Tosh and Kemp 1994). According to Roff (2002), antagonistic pleiotropy has long been considered a probable mechanism for the maintenance of genetic variance. Inclusion of sire year interaction in the model could lead to reduction in the negative correlation between the animal effects (Robinson 1996; Berwegeret *al.* 1999). The data structure in the present study has not included this interaction. One more peculiar thing observed for pre weaning traits was large negative estimate of r_{am}, direct and maternal estimates tend to be higher than in models that assume σ_{am} to be zero. As noted by Notter and Hough (1997), estimates that don't involve r_{am} can be properly used for genetic prediction only if the user also accepts and incorporate the additive maternal covariance into the prediction model.

Correlations among body weight at different ages

The estimates of different correlations among body weights at different ages are presented in Table 3. Genetic correlations among body weights at different ages were positive and ranged from medium to high except correlations between BW-6W, BW-9W and BW-YW, for which negative r_g was estimated (Table 3). In, general, all the estimates were significantly different from zero. High genetic correlations between body weight traits suggest that many of the genetic factors that influence body weight at weaning to adult stage were the same.

The phenotypic correlations among body weights at different ages were positive and medium to high in magnitude. The phenotypic correlations were high between adjacent weights and declined in magnitude as the interval between the weights being related increased (Table 3). The significantly high phenotypic correlation (among 6W, 9W and YW) at this stage indicated that a lamb weighted heavier at 6 months of age, was likely to be heavier at 9 and 12 months of age. In the field condition, the earliest

Table 3: Correlation estimates among body weight traits under bivariate animal models.

Trait	r_g	r_p	r_m	r_e
BW-WW	0.132±0.138	0.297±0.013	0.045 ±0.306(rc = 0.984**±0.180)	0.279±0.019
BW-6W	-0.005 ±0.114	0.228±0.015	0.713* ±0.448	0.290 ±0.021
BW-9W	-0.087±0.114	0.227±0.016	0.746*±0.381	0.307±0.022
BW-YW	-0.087±0.127	0.204±0.017	0.774**±0.327	0.259±0.024
WW-6W	0.735*±0.053	0.675*±0.008	0.999**±0.109	0.655*±0.013
WW-9W	0.545± 0.075	0.564±0.011	0.998**±0.204	0.565±0.016
WW-YW	0.590±0.082	0.497±0.013	0.877**±0.251	0.473±0.019
6W-9W	0.795**±0.032	0.774**±0.007	0.885**±0.454	0.766**±0.010
6W-YW	0.696*±0.050	0.649*±0.010	0.997**±0.425	0.630* ±0.016
9W-YW	0.914**±0.023	0.772**±0.007	0.996** ±0.265	0.721*±0.012

r_g- additive genetic correlation, r_p-phenotypic correlation, r_m-maternal additive genetic correlation, r_c-maternal permanent environmental correlation and r_e-residual correlations; ** - Highly significant (P≤0.01) ; * - Significant (P≤0.05)

age at which sheep are purchased is around six months and hence weight at six months would be important criteria for evaluation of lambs in field conditions. The findings were in close agreement with the findings of Gowane *et al.* (2010) in Malpura and Parihar *et al.* (2017) in Magra sheep.

Only two traits *i.e.* birth weight and weaning weight showed maternal permanent environmental correlation in present study. This result indicates that in the existing management conditions, good maternal environment pose positive effects on lambs from birth to weaning stage. The highest maternal correlation between WW and 6W (0.999±0.109) was estimated highly positive and significant in present study. Maternal genes sharing dependence gradually declines as is evident from the decline are genetic correlation of maternal effects as the animal grows.

CONCLUSION

For formulation of breeding programmes at any farm/ research station, there is requirement of accurate values of genetic parameters and (co)variance components. An animal model like DFREML takes into accounts all relationship in the pedigree and is therefore expected to provide estimates of genetic parameters with higher precision. The study revealed that the moderate heritability indicates that modest rates of genetic progress may be possible for these traits from selection under the prevailing management system. The maternal influence diminished as age increases and maternal genetic effect was found to be important and sizeable at weaning stage. It is more useful to use the total heritability for evaluation of the response for selection based on phenotypic values to prevent the use of biased estimates of additive heritability caused by high and negative correlation between additive and maternal effect.

Conflict of interest

Authors declare that there is no conflict of interest for this work.

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