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Genetic parameters for Kleiber ratio and its relation to other body weight traits in Nilagiri and Sandyno sheep

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ABSTRACT

Kleiber ratio (KR) is an indicator of growth efficiency irrespective of body size. The trait was recommended as an efficient indirect selection criterion. The present study was done to estimate genetic parameters for KR and explore the possibility of its use as a selection criterion in Nilagiri and Sandyno sheep. KR for the pre-weaning (birth to 3-months) and post-weaning (3– 6, 6–9, 9–12 and 3–12 months) periods was studied. Pre-weaning KR was much higher than post-weaning KR in both the breeds. The mean pre-weaning KR for Nilagiri and Sandyno sheep was 14.37 and 14.52, respectively. All the post-weaning KR values were less than six. Animal model including or ignoring maternal effects was used to obtain REML estimates of (co)variances. The best model was chosen based on log-likelihood ratio test. Maternal effects and inbreeding were not significant for KR at any of the age intervals. Moderate estimates of heritability were obtained for pre-weaning KR in both the breeds. Among the post-weaning KR, the age interval from 3–6 months and 3–12 months showed moderate values in Nilagiri sheep. Post-weaning KR for Sandyno sheep showed negligible to low heritability estimates. The maximum heritability of 0.143 was for KR 3–6 months in Nilagiri sheep. In Nilagiri sheep, genetic correlation between pre-weaning KR and body weight traits ranged from 0.634 to 0.875. Similarly, in Sandyno sheep, the values ranged from 0.883 to 0.959. Thus pre-weaning KR could be used as a criterion for indirect selection to improve important body weight traits.

Key words: Growth, Indirect selection, Maternal effect, Nilagiri, Sandyno

Nilagiri sheep, native to the Nilagiri hills of Tamil Nadu is known for its adaptability to high altitude, low input system of rearing and dual utility (fine wool and meat). Recently, the breed has been found to possess the FecB mutation known for its prolificacy (Sudhakar *et al.* 2013). Sandyno sheep is a synthetic breed developed from Nilagiri sheep. The demand for wool in the region is less and these animals are primarily maintained for meat. It was reported that KR has high phenotypic correlation with feed efficiency in beef cattle and was suggested as an efficient indirect selection criterion under extensive production systems (Scholtz and Roux 1988).

Studies on various sheep breeds have shown that direct and maternal genetic effects are important for growth traits, including KR (Maria *et al.* 1993, Abegaz *et al.* 2005, Ghafouri-Kesbi *et al.* 2011). World over, there are only a few studies on genetic evaluation of KR, especially those including maternal effects. Among Indian breeds, the only genetic study including maternal genetic components on KR was in Malpura sheep (Prakash *et al.* 2012). The present study was done to estimate direct and maternal genetic (co)variance components for KR and analyse relationship of the trait with other important growth traits in Nilagiri and Sandyno breeds of sheep.

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MATERIALS AND METHODS

The present study was based on data pertaining to Nilagiri and Sandyno animals born at the Sheep Breeding Research Station, Sandynallah. Pedigree information available from 1965 to 2011 (Table 1) and growth data recorded from 1992 to 2011 were collected from records maintained at the station.

The farm is situated at an altitude ranging from 2,090 to 2,235 m above mean sea level. The mean minimum and

Table 1. Pedigree information for Nilagiri and Sandyno populations

Parameter	Nilagiri	Sandyno
Number of animals	5051	9921
Number of founders (base population)	759	2018
Number of animals with both parents known	4292	7903
Number of sires	309	458
Number of dams	966	1344

maximum temperatures recorded were 12.2° and 19.2°C respectively, and the range was from 8.5°C in January to 22.1°C in April. Sub-zero temperatures were also recorded on individual days during winter.

Nilagiri sheep were maintained by pure breeding under selection. The breed composition and formation of the Sandyno breed of sheep is presented in Table 2. The system of management was semi–intensive with concentrate at the rate of 150g/animal/day fed in addition to grazing. Based on the climatic conditions, lambing was planned for two seasons in a year.

Kleiber ratio (KR) for the pre-weaning (birth to 3-months) and post-weaning (3–6, 6–9, 9–12 and 3–12 months) periods were calculated as follows:

$$KR = ADG/W^{0.75}$$

Where, ADG, average daily gain for the period expressed in g/day; $W^{0.75}$, metabolic body weight at the older age of the period for which KR is calculated.

The other traits studied were weight at birth (BW), 3 (WW), 6 (6W), 9 (9W) and 12 (YW) months of age and pre and post- weaning average daily gain (ADG). Weaning was practiced at 90 days of age and post-weaning period was up to 1 year of age. The various fixed effects included were contemporary groups (CG) of lambs born during a particular year and season (39 groups), the age of dam at lambing with six levels (< 2 yr, 3yr, 4 yr, 5yr, 6 yr and > 6yr), litter size at birth (single, twins and triplets), sex of lamb and inbreeding (5 classes with F values of 0, up to 5, >5 up to 10, >10 up to 15 and >15 %). The effects of various fixed factors were analysed by least squares method under a univariate general linear model.

(Co) variance components for different KR and growth traits were estimated by Restricted Maximum Likelihood (REML) using the WOMBAT programme of Meyer (2007), by fitting an animal model throughout. Separate analyses were carried out for Nilagiri and Sandyno sheep. Six different single trait linear models which accounted for the direct and maternal effects, allowing for and ignoring genetic covariance between direct and maternal effects were fitted initially.

Statistical models

$Y = Xb + Z_a a + e$ (Model 1)

$Y = Xb + Z_a a + Z_p p + e$ (Model 2)

$Y = Xb + Z_a a + Z_m m + e$ with Cov (a, m) = 0 (Model 3)

$Y = Xb + Z_a a + Z_m m + e$ with Cov (a, m) = $A\sigma_{am}$ (Model 4)

$Y = Xb + Z_a a + Z_m m + Z_p p + e$ with Cov (a, m) = 0 (Model 5)

$Y = Xb + Z_a a + Z_m m + Z_p p + e$ with Cov (a, m)=$A\sigma_{am}$ (Model 6)

Where, 'Y' is a N × 1 vector of records, 'b' denotes the fixed effects in the model with association matrix X, 'a' is the vector of direct genetic effects with the association matrix Z_a, 'm' is the vector of maternal genetic effects with the association matrix Z_m, 'p' is the vector of permanent maternal environmental effects with the association matrix Z_p, and 'e' denotes the vector of residual (temporary environment) effect. Cov (a, m) is the covariance between the direct genetic effect and maternal effect. The fixed effects included in the model were those found to have significant effect in the initial least-squares analyses.

Log likelihood ratio tests (LRT) were carried out to identify the best model for each trait. Genetic correlations among KR at various age intervals and between KR and different growth traits were obtained through bivariate analyses. The fixed effects included were same as those included in the univariate animal model analyses (Models 1 to 6). The random effects to be included were decided from the best model determined through LRT. The variance components estimated from univariate analyses were used as starting values. Sampling errors for variance ratios and correlations were obtained from the approximations as described by Meyer (2007).

RESULTS AND DISCUSSION

The least-squares means of KR at various age intervals for Nilagiri and Sandyno sheep are presented in Table 2. In both the populations, high values (>14) were obtained for

Table 2. Least-squares means (±SE) of pre- and post-weaning Kleiber ratio in Nilagiri and Sandyno sheep

Details	Pre-weaning KR		Post-weaning KR							
			3-6 months		6-9 months		9-12 months		3–12 months	
	n	Mean	n	Mean	n	Mean	n	Mean	n	Mean
Overall mean	6504	14.45±0.16	4309	5.77±0.19	3267	3.77±0.22	2978	3.76±0.21	3257	3.63±0.10
Breed		**		**		**		**		**
Nilagiri	2831	14.37±0.16	1951	5.62±0.19	1445	3.72±0.22	1336	3.72±0.21	1463	3.56±0.10
Sandyno	3673	14.52±0.16	2358	5.93±0.20	1822	3.82±0.22	1642	3.80±0.22	1794	3.71±0.10
Sex		**		**		**		**		**
Male	3269	14.59±0.16	1941	5.88±0.19	1447	3.95±0.22	1256	4.20±0.21	1357	3.82±0.10
Female	3235	14.30±0.16	2368	5.67±0.19	1820	3.60±0.22	1722	3.31±0.21	1900	3.45±0.10
Type of birth		**		**		NS		NS		**
Single	5519	14.22^b±0.09	3708	5.36^b±0.12	2837	3.65±0.13	2598	3.82±0.13	2841	3.44^b±0.06
Twin	958	14.63^a±0.11	582	5.68^b±0.14	419	3.86±0.16	369	4.00±0.16	405	3.62^a±0.07
Triplet	27	14.49^{ab}±0.39	19	6.28^a±0.47	11	3.81±0.53	11	3.46±0.50	11	3.84^a±0.23

**, (P<0.01); NS, nonsignificant.

pre-weaning interval from birth to 3-months, while the KR values for all the post-weaning age intervals were lower than six. Similar findings were observed in other studies for Malpura (Prakash *et al.* 2012), Horro (Abegaz *et al.* 2005), Sanjabi (Mohammadi *et al.* 2010), Karakul (Talebi 2012) and Zandi (Ghafouri-Kesbi *et al.* 2011) sheep. Pre-weaning KR in Nilagiri and Sandyno sheep were lower than those reported for Arman, Horro, Karakul, Sanjabi and Zandi sheep (Table 2). Very high pre-weaning KR of 18.51 was noticed in Arman sheep (Mokhtari *et al.* 2012). The post-weaning KR for the period 3–6 months found in this study was higher than that for Horro sheep (Abegaz *et al.* 2005) and lower than those for Malpura (Prakash *et al.* 2012), Sanjabi (Mohammadi *et al.* 2010), Karakul (Talebi 2012) and Zandi (Ghafouri-Kesbi *et al.* 2011) sheep.

KR was lowest for the post-weaning period from 9 to 12 months of age. Majority of the lambs reached their 9W during lean season of winter, which extends up to one year of age. The weight of lambs at both these limits (9 and 12 months) is less, leading to lesser weight gain during the period. Sandyno breed had better KR values than Nilagiri sheep at pre- and post-weaning stages.

The ¾ power of body weight was identified as a suitable unit for the metabolic body size (Kleiber 1947). KR, calculated as the ratio of ADG to that of metabolic body weight at the latter age of the interval (and named after Kleiber) gives an indication of growth efficiency independent of body size. Inspite of the fact that Sandyno is superior to Nilagiri in terms of body weight traits, there was not much difference in KR between the 2 breeds. It was reported that Kleiber ratio has high phenotypic correlation with feed efficiency in beef cattle and was suggested as an efficient indirect selection criterion for feed efficiency under extensive production systems (Scholtz and Roux 1988).

The effect of various factors on KR was found to be similar in Nilagiri and Sandyno sheep. Initial least squares analysis revealed that CG, sex and season had significant influence on KR at all the age intervals. Similar observations were reported in other breeds of sheep (Mohammadi *et al.* 2010, Ghafouri-Kesbi *et al.* 2011). Type of birth and age of dam at lambing were found to influence pre-weaning KR and KR for the earlier post-weaning intervals of 3–6 and 3–12 months significantly. Inbreeding did not have significant effect on KR for any of the age intervals and thus not included in the models for estimation of variance components.

The (co) variance components and heritability estimates inclusive of direct genetic (h^2), maternal permanent environmental (c^2) and total heritability (h^2_t) for KR at different age intervals, estimated from the best model for Nilagiri and Sandyno sheep are presented in Table 3. In Nilagiri and Sandyno sheep, for pre-weaning KR, model 2 with maternal permanent environmental effect in addition to the direct genetic effect was the best model chosen through LRT. Mokhtari *et al.* (2012) also found similar results for Arman sheep. In Horro (Abegas *et al.* 2005) and Zandi (Ghafouri-Kesbi *et al.* 2011)) sheep, maternal genetic effects were found to influence pre-weaning KR. Other studies in Malpura (Prakash *et al.* 2012) and Sanjabi (Mohammadi *et al.* 2010) sheep showed absence of maternal genetic or permanent environmental effects on the trait.

For all the post-weaning KR, the basic model 1 with direct genetic effect alone as random effect was most significant. Similar findings were reported in other breeds of sheep (Abegas *et al.* 2005, Mohammadi *et al.* 2010, Ghafouri-Kesbi *et al.* 2011, Prakash *et al.* 2012). The only exception was KR 3–12 months in Sandyno sheep, where model 2 was most significant. Models including maternal genetic effect or correlation between direct and maternal genetic effect (σ_{am}) were not significant for KR at any of the intervals.

Among the KR at various age intervals, highest estimate of h^2 was observed for post-weaning KR 3–6 m (0.143) in Nilagiri. Prakash *et al.* (2012) reported a slightly lower value

Table 3. (Co) variance components estimated from the best model and genetic parameters for growth traits in Nilagiri and Sandyno sheep

Trait	Model	σ^2_e	σ^2_p	h^2±SE	e^2±SE	m^2±SE
			Nilagiri			
Pre-weaning KR	2	3.249	3.958	0.106±0.032	0.073±0.019	-
KR 3-6 months	1	3.388	3.953	0.143±0.038	-	-
KR 6-9 months	1	2.927	3.033	0.035±0.032	-	-
KR 9-12 months	1	2.309	2.427	0.048±0.031	-	-
KR 3-12 months	1	0.477	0.532	0.103±0.039	-	-
			Sandyno			
Pre-weaning KR	2	3.101	3.869	0.109±0.026	0.090±0.018	-
KR 3-6 months	1	3.604	3.724	0.032±0.023	-	-
KR 6-9 months	1	2.590	2.720	0.048±0.026	-	-
KR 9-12 months	1	2.493	2.531	0.015±0.024	-	-
KR 3-12 months	2	0.492	0.527	0.003±0.022	0.063±0.027	-

σ^2_e, error variance; σ^2_p, phenotypic variance; h^2, direct heritability; c^2, maternal permanent environmental variance ratio; m^2, maternal heritability.

Table 4. Genetic correlation of Kleiber ratio with other growth traits in Nilagiri and Sandyno sheep

Trait	BW	WW	6W	9W	YW	Pre-ADG	Post-ADG
			Nilagiri				
Pre-weaning KR	0.406±0.151	0.766±0.077	0.875±0.064	0.827±0.076	0.634±0.126	0.843±0.053	0.370±0.197
KR 3-6 months	-0.258±0.197	-0.397±0.176	0.291±0.254	0.238±0.196	0.380±0.194	-0.324±178	0.746±0.139
KR 6-9 months	0.198±0.306	0.643±0.479	0.828±0.662	0.783±0.428	0.960±0.424	0.628±0.509	0.723±0.354
KR 9-12 months	0.109±0.293	-0.692±0.299	-0.606±0.387	-0.764±0.223	-0.517±0.299	-0.778±0.280	-0.124±0.333
KR 3-12 months	-0.014±0.208	-0.082±0.233	0.343±0.268	0.183±0.236	0.542±0.181	-0.006±0.229	0.903±0.047
			Sandyno				
Pre-weaning KR	0.673±0.122	0.882±0.043	0.940±0.049	0.959±0.050	0.883±0.082	0.940±0.021	0.910±0.395
KR 3-6 months	0.640±0.241	-0.820±0.350	-0.391±0.511	-0.932±0.719	-0.472±0.482	-0.514±0.285	0.049±0.624
KR 6-9 months	0.805±0.259	0.080±0.255	0.106±0.284	0.159±0.285	0.262±0.266	-0.009±0.254	0.179±0.652
KR 9-12 months	0.795±0.382	-0.250±0.549	-0.150±0.643	0.444±0.682	0.457±0.661	-0.152±0.522	1.000±0.577
KR 3-12 months	0.859±0.129	-0.837±f	0.593±f	-0.265±f	0.362±f	-0.250±f	0.606±f

f, approximations for standard error failed.

Table 5. Genetic and phenotypic correlations (±S.E.) among Kleiber ratio at different age intervals in Nilagiri and Sandyno sheep

Trait	Pre-weaning KR	KR 3-6 months	KR 6-9 months	KR 9-12 months	KR 3-12 months
			Nilagiri[a]		
Pre-weaning KR	-	-0.285 0.183	0.572 0.522	-0.813 0.285	-0.056 0.233
KR 3-6 months	-0.358 0.022	-	0.015 0.409	0.066 0.320	0.926 0.096
KR 6-9 months	-0.077 0.028	-0.189 0.027	-	0.237 0.768	0.427 0.381
KR 9-12 months	-0.167 0.029	-0.021 0.029	-0.223 0.029	-	0.346 0.315
KR 3-12 months	-0.434 0.023	0.579 0.018	0.294 0.026	0.401 0.024	-
			Sandyno[a]		
Pre-weaning KR	-	-0.228 0.268	-0.051 0.258	-0.187 0.534	-0.890 f
KR 3-6 months	-0.320 0.020	-	-0.115 0.435	0.872 0.905	0.879 0.486
KR 6-9 months	-0.092 0.025	-0.163 0.024	-	0.677 0.708	0.201 f
KR 9-12 months	-0.044 0.027	-0.050 0.025	-0.150 0.026	-	nc
KR 3-12 months	-0.380 0.022	0.540 0.017	0.345 0.022	nc	-

a, For each breed, values above diagonal are genetic correlations and those below diagonal are phenotypic correlations. f, the approximations for standard error failed; nc, no convergence.

of 0.12 for post-weaning KR 3–6 months in Malpura sheep. Heritability estimates for pre-weaning KR were moderate and similar in Nilagiri (0.106) and Sandyno (0.109) sheep. Moderate values of heritability in these early KR traits provide scope for genetic improvement. Comparing the estimates from models that included maternal effect in earlier studies, the value of direct heritability for pre-weaning KR in the present study was comparable to that found in Zandi sheep (Ghafouri-Kesbi *et al.* 2011). Higher values than those in the present study were reported for Malpura (Prakash *et al.* 2012) and Sanjabi (Mohammadi *et al.* 2010) sheep, while lower estimates were found in Arman (Mokhtari *et al.* 2012) and Horro (Abegaz *et al.* 2005) breeds of sheep.

The estimate for post-weaning KR 3–12 months was moderate (0.103) in Nilagiri sheep, while the value was almost negligible (0.003) in Sandyno sheep. Heritability values for post-weaning KR at other age intervals were low with values less than 0.05. Estimates of h^2 obtained for post-weaning KR in other breeds of sheep like Horro, Sanjabi and Zandi sheep were also low, but ranged between 0.05 and 0.08. (Abegas *et al.* 2005, Mohammadi *et al.* 2010, Ghafouri-Kesbi *et al.* 2011). Since, maternal genetic effect had no influence on any of the traits, h^2 and h^2_t were same.

The estimates of genetic correlation between KR and different body weight traits are presented in Table 4. Pre weaning KR had moderate to high genetic correlation with all the body weight traits in both the breeds. The positive genetic correlation of the trait with body weight traits like 9W and YW, which are important from economic point of view, provides good scope for indirect selection using pre-weaning KR. Other studies in Sanjabi, Armaan and Malpura breeds of sheep also showed similar results (Mohammadi *et al.* 2010, Mokhtari *et al.* 2012, Prakash *et al.* 2012).

The estimates of genetic and phenotypic correlation among KR at different age intervals are presented in Table 5. In Nilagiri sheep, pre-weaning KR had high negative genetic correlation with KR 9–12 months and moderate positive correlation with KR 6–9 months. In Sandyno sheep, pre-weaning KR had high negative correlation with KR 3–12 months of age. In general, pre-weaning KR had negative genetic correlation with post-weaning KR. Mohammadi *et* *al.* (2010) and Ghafouri-Kesbi *et al.* (2011) found similar results in Sanjabi and Zandi sheep, respectively. Prakash *et al.* (2012) observed negligible correlation between pre-weaning and post-weaning KR in Malpura sheep of India.

Venkataramanan (2013) indicated low to moderate heritability for body weight traits, especially for those available early in age (WW and 6W). Selecting animals based on traits available latter in age results in loss due to maintaining the entire stock for longer duration. The body weight at latter ages (9W and YW) are important from economic point of view, improvement can be brought about by selection based on traits available early in age. High genetic correlations between pre-weaning KR and these economically important body weight traits in Nilagiri and Sandyno sheep provide good scope for indirect selection in both the breeds.

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