

Research Article

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Evaluating animal models comprising direct and maternal effects associated with growth rates and the Kleiber ratio in Harnali sheep

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Summary

The present work evaluated animal models comprising direct and maternal effects to estimate (co)variance components and genetic parameters of growth rates and Kleiber ratio in Harnali sheep. The information on pedigree and targeted traits of 1862 lambs born to 144 sires and 591 dams was collected for the period from 1998 to 2018. The traits studied were average daily gain from birth to 3 months of age (ADG₁), 3 months to 6 months of age (ADG₂), and 6 months to 12 months of age (ADG₃) and their corresponding Kleiber ratios as KR₁, KR₂ and KR₃, respectively. The statistical methods included the general linear model for analyzing the effects of fixed factors and animal models for deriving variance components for targeted traits. According to best model evaluated on the basis of likelihood ratio test, the estimated direct heritability was low in magnitude and ranged from 0.04 to 0.14. Direct heritability estimates for ADG₁, ADG₂, ADG₃, KR₁, KR₂ and KR₃ were 0.06, 0.14, 0.05, 0.04, 0.11 and 0.05, respectively. The maternal genetic effects contributed (4–7%) significantly for ADG₁, KR₁ and KR₂ traits. The genetic correlations ranged from -0.35 ± 0.11 (ADG₁-KR₂) to 0.98 ± 0.01 (ADG₂-KR₂ and ADG₃-KR₃) and phenotypic correlations ranged from -0.36 ± 0.02 to 0.98 ± 0.01 for ADG₁-KR₂ and ADG₂-KR₂, respectively. The significant maternal effects along with low levels of direct effects for average daily gain and Kleiber ratio at different age group should be considered while setting selection and managerial strategies to achieve anticipated growth rates in Harnali sheep.

Introduction

Sheep production systems play a crucial role in the livelihood security of millions of people in arid and semi-arid regions of India. Growth rate is the most important component for improving the efficiency of the sheep industry. Considering the variation between the growth rates of different lambs, it may be possible to partition into genetic and environmental parts to identify the potential of a particular trait for selection strategies. Selection using average daily gain (ADG) is an important selection criterion for boosting the production and profitability of a sheep (Abegaz *et al.*, 2005; Mohammadi *et al.*, 2013). Along with ADG, feed conversion efficiency is also another important aspect for framing any selection strategy especially considering from the points of view of economics and market output. Kleiber (1947) provided the Kleiber ratio (KR) as a measure of feed conversion efficiency or growth efficiency. Although, ADG and KR are positively associated with each other, KR predicts feed conversion more accurately than ADG by accounting for the metabolic weight of an animal (Scholtz *et al.*, 1990; Badenhorst, 2011).

For a particular trait of interest, the estimates of the genetic variation are not rigid. The animal models accounting for maternal effects (genetic/environmental), along with direct effects, may provide unbiased estimates of variance components for a trait (Ekiz, 2005; Kariuki *et al.*, 2010; Prince *et al.*, 2010; Bangar *et al.*, 2020). However, many factors, including size of population and environmental conditions, may fluctuate the direct effects and maternal effects associated with these traits. Therefore, consistent and unbiased estimates of direct and maternal effects by assessing animal models with stringent evaluation criteria are a pre-requisite to maximize genetic gain for economically important traits (Eskandarinasab *et al.*, 2010; Tesema *et al.*, 2020).

After consideration of the above-mentioned inducements, the present study was conducted to estimate (co)variance components and genetic parameters for growth rate and KR in Harnali sheep using animal models.

Materials and methods**Animal resource and targeted traits**

Harnali sheep are a newly developed synthetic dual-purpose strain. The chief attributes of Harnali are superior carpet wool and better growth performance. It is a three-breed cross from 62.5% exotic inheritance (Russian Merino and Corriedale) and 37.5% Nali. Photographs of a



Figure 1. Harnali female



Figure 2. Harnali male

Harnali female and a Harnali male are presented in Figure 1 and Figure 2, respectively. The data for the present investigation, extending over a period of 21 years, from 1998 to 2018 were collected from the history and pedigree sheets maintained at a sheep breeding farm, LUVAS, in Hisar (India). The targeted growth rates were generated using weights at different stages, namely average daily gain (in grams) from birth weight to 3 months of age (ADG_1), 3 months to 6 months of age (ADG_2), and 6 months to 12 months of age (ADG_3). The growth efficiency in terms of Kleiber ratio was also calculated as $KR_1 = ADG_1/WWT^{0.75}$, $KR_2 = ADG_2/6WT^{0.75}$, and $KR_3 = ADG_3/YWT^{0.75}$.

Table 1. Six univariate models including or excluding maternal effects

Model number	Model
1	$y = X\beta \pm Z_1a \pm e$
2	$y = X\beta \pm Z_1a \pm Z_2m \pm e$ with $Cov(a, m) = 0$
3	$y = X\beta \pm Z_1a \pm Z_2m \pm e$ with $Cov(a, m) = A\sigma_{am}$
4	$y = X\beta \pm Z_1a \pm Z_3c \pm e$
5	$y = X\beta \pm Z_1a \pm Z_2m \pm Z_3c \pm e$ with $Cov(a, m) = 0$
6	$y = X\beta \pm Z_1a \pm Z_2m \pm Z_3c \pm e$ with $Cov(a, m) = A\sigma_{am}$

where y is the vector of observations; β , a , m , c and e are vectors of fixed, direct additive genetic, maternal additive genetic, maternal permanent environmental effects, and residual effects, respectively; with respective association matrices X , Z_1 , Z_2 , and Z_3 ; A is the numerator relationship matrix between animals; and σ_{am} is the covariance between additive direct and maternal genetic effects.

Statistical analysis

A general linear model consisting of the fixed effects of year of birth in seven classes (1998–2018) with each class comprising 3 years, sex of lamb in two classes (male and female) and the dam's weight at lambing in three classes (21–27.9, 28.0–30.0 and 30.1–43 kg) was used to determine the significant influences of these factors on targeted traits. Total variation among the targeted traits was subjected for partitioning into direct additive, maternal genetic, maternal permanent environmental and residual variation using the restricted maximum likelihood method (AI-REML) and WOMBAT software (Meyer, 2007). The six univariate models including or excluding maternal effects, which were fitted to estimate genetic covariance components and corresponding heritability for each trait are given in Table 1. Maternal repeatability was estimated as per Al-Shorepy (2001). The total heritability was also estimated as per the formula given by Willham (1972). The evaluation of different animal models was carried out using the log-likelihood test (Prince *et al.*, 2010).

Results

The characteristics of data structure, i.e. the number of individuals, number of sires and dams, mean, standard deviations and coefficient of variation for respective traits, are summarized in Table 2. Mean values accounted for ADG_1 , ADG_2 , ADG_3 , KR_1 , KR_2 and KR_3 and were 109.13 g, 49.90 g, 35.06 g, and 15.65, 5.72 and 3.18, respectively.

Estimates of (co)variance components, additive and maternal genetic parameters obtained in most suitable models, along with their log-likelihood values are presented in Table 3. For traits ADG_1 , KR_1 and KR_2 , model 2 accounting for direct and maternal effects was found to be the most appropriate. This included growth rate and feed conversion efficiency during the pre-weaning period that was significantly influenced by individual as well as by maternal genes. Whereas, for remaining traits, the most suitable model was model 1. Estimates of direct effects in terms of direct heritability (h^2) for ADG_1 , ADG_2 , ADG_3 , KR_1 , KR_2 and KR_3 resulting from best model were 0.06 ± 0.03 , 0.14 ± 0.04 , 0.05 ± 0.03 , 0.04 ± 0.03 , 0.11 ± 0.04 and 0.05 ± 0.03 , respectively. The estimates of maternal effects (m^2) for ADG_1 , KR_1 and KR_2 were 0.07 ± 0.02 , 0.06 ± 0.02 and 0.04 ± 0.02 , respectively.

The estimates of genetic and phenotypic correlations for targeted traits are shown in Table 4. The genetic correlation estimates for the studied traits were in the range from -0.35 ± 0.11 (ADG_1 - KR_2) to 0.98 ± 0.01 (ADG_2 - KR_2 and ADG_3 - KR_3). The estimated

Table 2. Characteristics of data structure for traits under study of Harnali sheep

Traits	ADG1	ADG2	ADG3	KR1	KR2	KR3
Number of records	1862	1754	1550	1862	1754	1550
Sires with progeny records	144	144	138	144	144	138
Progeny per sire	12.93	12.18	11.23	12.93	12.18	11.23
Dams with progeny records	591	575	540	591	575	540
Progeny per dam	3.15	3.05	2.87	3.15	3.05	2.87
Mean	109.13	49.90	35.06	15.65	5.72	3.18
Standard deviation	29.16	25.63	17.65	1.87	2.64	1.39
Coefficient of variation (%)	26.72	51.37	50.34	11.93	46.22	43.75

ADG₁: Average daily gain from birth to 3 months of age; ADG₂: Average daily gain from 3 months to 6 months of age; ADG₃: Average daily gain from 6 months to 12 months of age; KR₁: Kleiber ratio associated with ADG₁; KR₂: Kleiber ratio associated with ADG₂; KR₃: Kleiber ratio associated with ADG₃.

Table 3. Genetic parameter estimates for traits studied fitting the most appropriate model

Traits	Best model	σ^2_a	σ^2_m	σ^2_e	σ^2_p	$h^2 \pm S.E.$	$m^2 \pm S.E.$	h^2_t	t_m	Log-L
ADG ₁	2	36.45	41.88	520.87	599.20	0.06 \pm 0.03	0.07 \pm 0.02	0.10	0.09	-6861.98
ADG ₂	1	88.59	-	549.94	638.53	0.14 \pm 0.04	-	0.14	0.03	-6519.01
ADG ₃	1	13.98	-	286.81	300.79	0.05 \pm 0.03	-	0.05	0.01	-5192.86
KR ₁	2	0.12	0.16	2.51	2.79	0.04 \pm 0.03	0.06 \pm 0.02	0.07	0.07	-1882.48
KR ₂	2	0.74	0.27	5.67	6.68	0.11 \pm 0.04	0.04 \pm 0.02	0.13	0.07	-2526.33
KR ₃	1	0.10	-	1.75	1.85	0.05 \pm 0.03	-	0.05	0.01	-1258.45

σ^2_a : Direct genetic variance; σ^2_m : Maternal additive genetic variance; σ^2_e : Residual variances; σ^2_p : Phenotypic variances; $h^2 \pm S.E.$: Direct heritability; $m^2 \pm S.E.$: Maternal heritability; h^2_t : Total heritability; t_m : Repeatability of ewe performance; Log-L: Log-likelihood for the best model.

Table 4. Genetic (above diagonal) and phenotypic (below diagonal) correlation (\pm SE) among growth rate and KR in Harnali sheep

Traits	ADG ₁	ADG ₂	ADG ₃	KR ₁	KR ₂	KR ₃
ADG ₁		-0.19 \pm 0.11	-0.11 \pm 0.14	0.91 \pm 0.02	-0.35 \pm 0.11	-0.20 \pm 0.13
ADG ₂	-0.23 \pm 0.02		-0.25 \pm 0.13	-0.11 \pm 0.11	0.98 \pm 0.01	-0.32 \pm 0.13
ADG ₃	-0.04 \pm 0.03	0.03 \pm 0.03		-0.14 \pm 0.14	-0.20 \pm 0.13	0.98 \pm 0.01
KR ₁	0.95 \pm 0.01	-0.20 \pm 0.02	-0.04 \pm 0.02		-0.24 \pm 0.12	-0.20 \pm 0.14
KR ₂	-0.36 \pm 0.02	0.98 \pm 0.01	0.07 \pm 0.02	-0.32 \pm 0.02		-0.24 \pm 0.13
KR ₃	-0.07 \pm 0.03	0.00 \pm 0.03	0.98 \pm 0.00	-0.07 \pm 0.03	0.06 \pm 0.03	

ADG₁: Average daily gain from birth to 3 months of age; ADG₂: Average daily gain from 3 months to 6 months of age; ADG₃: Average daily gain from 6 months to 12 months of age; KR₁: Kleiber ratio associated to ADG₁; KR₂: Kleiber ratio associated to ADG₂; KR₃: Kleiber ratio associated to ADG₃.

genetic correlation between ADG and their respective KR at the same age was found to be significantly high and positive, i.e. ADG₁-KR₁ (0.91 \pm 0.02), ADG₂-KR₂ (0.98 \pm 0.01) and ADG₃-KR₃ (0.98 \pm 0.01). All the remaining traits were negatively correlated to each other. The estimates of phenotypic correlation ranged from -0.36 \pm 0.02 to 0.98 \pm 0.01 for ADG₁-KR₂ and ADG₂-KR₂, respectively. For aspects of phenotypic correlation between pre-weaning traits, ADG₁-KR₁ were positively correlated (0.95 \pm 0.01). ADG₁ and KR₁ were positively correlated with post-weaning average daily gains (ADG₂ and ADG₃) and post-weaning Kleiber ratio (KR₂ and KR₃). ADG₂-KR₂ and ADG₃-KR₃ were also

found to be positively correlated, 0.98 \pm 0.01 and 0.98 \pm 0.00, respectively.

Discussion

Average daily gain from birth to 3 months of age (ADG₁)

For this trait, the maternal heritability was slightly more than direct heritability (0.07 vs. 0.06). This indicated that genes contributing to maternal performance had an equivalent effect on the early growth rate of lambs. Higher estimates of direct heritability (h^2) for ADG₁

were published by Savar-Sofla *et al.* (2011) in Moghani (0.21), Prakash *et al.* (2012) in Malpura (0.23), Ghafouri-Kesbi (2013) in Mehraban (0.10), Mandal *et al.* (2015) in Muzaffarnagari (0.15), Singh *et al.* (2016) in Marwari (0.26), Jafari and Razzagzadeh (2016) in Makuie (0.20), Kumar *et al.* (2018) and Illa *et al.* (2019) in Nellore (0.20 and 0.37, respectively) and Mahala *et al.* (2020) in Avikalin sheep (0.48). Bangar *et al.* (2020) reported 0.43 as estimate of direct heritability due to only direct effects of ADG_1 in Harnali sheep. The h^2 estimate reported by Gholizadeh and Ghafouri-Kesbi (2017) in Baluchi sheep (0.03) and Bangar *et al.* (2018) in Deccani sheep (0.07) was in agreement with the present findings. Ghafouri-Kesbi (2013), Jafari and Razzagzadeh (2016), Illa *et al.* (2019) and Mahala *et al.* (2020) calculated higher estimates of maternal heritability (m^2) for ADG_1 (0.10, 0.16 and 0.11, respectively). Whereas Mokhtari *et al.* (2012) reported an equivalent value (0.07) in Arman sheep, Ghafouri-Kesbi *et al.* (2011) reported lower maternal heritability (0.03) in Zandi sheep. The low level of additive variation and lesser estimates of h^2 in comparison with m^2 for ADG_1 indicated the prominence of maternal and environmental effects for desired growth at initial the stage of age. Results suggested that early growth rate was predominantly influenced by maternal behaviour.

Average daily gain from 3 months to 6 months of age (ADG_2)

Among all the models studied, models 3 and 6 showed higher estimates of Log-L values, in aspects of ADG_2 . Contrary trends between direct and maternal effects, due to negative covariance led to higher and negative estimates of r_{am} and biased estimates of h^2 . Estimates of h^2 under models 3 and 6 were exorbitant in comparison with models 1 and 2, which might be due to unrevealed effects of negative genetic covariance. Genetic covariance is restricted at higher negative magnitude, due to some concealed mechanism underlying the phenotypic relationship (Singh *et al.*, 2016). Therefore, we considered model 1 to be the most suitable in the present investigation, instead of model 3 or 6.

The estimate for h^2 for ADG_2 was in agreement with that reported by Prakash *et al.* (2012) and Singh *et al.* (2016) in Malpura and Marwari sheep, (0.13 and 0.16) respectively. Lower estimates were published by Savar-Sofla *et al.* (2011) in Moghani (0.02), Ghafouri-Kesbi (2013) in Mehraban (0.11), Gholizadeh and Ghafouri-Kesbi (2017) in Baluchi (0.11) and Bangar *et al.* (2020) in Harnali sheep (0.02). Kumar *et al.* (2018), Illa *et al.* (2019) and Mahala *et al.* (2020) recorded higher estimates as 0.24, 0.34 and 0.53, respectively in Nellore and Avikalin sheep. However, Bangar *et al.* (2018) reported similar findings (0.14) in Deccani sheep. The h^2 estimate observed for ADG_2 in the present study was low in magnitude, therefore selection based on this trait provided lesser scope for genetic improvement.

Average daily gain from 6 months to 12 months of age (ADG_3)

Very scant published literature is available for ADG from 6 months to 12 months of age. Higher h^2 estimates were reported by Singh *et al.* (2016), Kumar *et al.* (2018) and Mahala *et al.* (2020) in Marwari, Nellore and Avikalin sheep, (0.31, 0.17 and 0.34), respectively. Whereas, Bangar *et al.* (2020) reported a lower estimate (0.001) in Harnali sheep.

Kleiber ratios from birth to 3 months of age (KR_1)

By addition of the maternal additive genetic effect to the direct additive model, the log-likelihood value was found to be

significantly changed and led to low to moderate estimates of h^2 and m^2 for KR_1 . The low-level estimate of direct effect (h^2) was observed for this trait. Higher h^2 estimates were reported by Prakash *et al.* (2012) in Malpura (0.20), Ghafouri-Kesbi (2013) in Mehraban (0.13), Roshanfekar (2014) in Arabi (0.11), Mandal *et al.* (2015) in Muzaffarnagari (0.13), Jafari and Razzagzadeh (2016) in Makuie (0.20), Kumar *et al.* (2018) and Illa *et al.* (2019) in Nellore (0.25 and 0.48), Bangar *et al.* (2020) in Harnali (0.38) and Mahala *et al.* (2020) in Avikalin breeds (0.54). The h^2 estimate obtained in the present investigation agreed with those reported by Abegaz *et al.* (2005) in Horro (0.09), Mohammadi *et al.* (2011) in Zandi (0.05), Mokhtari *et al.* (2012) in Arman (0.04) and Bangar *et al.* (2018) in Deccani sheep (0.04).

The significant influence of maternal effects on KR_1 under model 2 was observed in this study, which was in accordance with m^2 estimates reported by Ghafouri-Kesbi *et al.* (2011) and Savar-Sofla *et al.* (2011) in Zandi and Moghani sheep (0.05). However, higher estimates 0.14, 0.24 and 0.21 were reported by Jafari and Razzagzadeh (2016), Illa *et al.* (2019) and Mahala *et al.* (2020), respectively.

Kleiber ratios from 3 months to 6 months of age (KR_2)

Similar to the KR_1 trait, KR_2 also influenced the direct additive effects and maternal genetic effects. This may be due to carry-over effects of maternal influence from the weaning period, which was also reported by Ghafouri-Kesbi (2013). Our estimate of direct effects for KR_2 was low in magnitude. However, lower h^2 estimates than our estimate have been reported for various sheep breeds by Eskandarinasab *et al.* (2010) in Afshari (0.06), Mohammadi *et al.* (2011) in Zandi (0.01) and Bangar *et al.* (2020) in Harnali (0.02) breeds. The present estimate was in agreement with that reported by Prakash *et al.* (2012) in Malpura (0.12), Ghafouri-Kesbi (2013) in Mehraban (0.13) and Bangar *et al.* (2018) in Deccani (0.16). Whereas Kumar *et al.* (2018) and Illa *et al.* (2019) in Nellore sheep and Mahala *et al.* (2020) in Avikalin sheep reported significantly higher estimates (0.23, 0.37 and 0.53, respectively). The estimate for m^2 for KR_2 matched the findings of Savar-Sofla *et al.* (2011) and Ghafouri-Kesbi (2013) (0.01 and 0.05, respectively). Whereas higher estimates were published by Illa *et al.* (2019) in Nellore sheep and Mahala *et al.* (2020) in Avikalin sheep (0.11 and 0.16, respectively).

Kleiber ratios from 6 months to 12 months of age (KR_3)

For KR_3 , only direct effects were sufficient to explain the genetic variation out of total variation. However, this estimate was found to be low for our resource population. Considerably higher h^2 estimates were published by Kumar *et al.* (2018) and Mahala *et al.* (2020) in Nellore (0.17) and Avikalin (0.39) sheep, respectively.

Our study was conducted using data from 1862 Harnali lambs for 21 years (1998 to 2018) and differed from that of Bangar *et al.* (2020), who used data records of 526 Harnali lambs for 5 years (2014–2018) in the following points:

- (1) We used a greater number of data records.
- (2) The period of our study was longer.
- (3) We observed significant maternal effects for ADG_1 , KR_1 and KR_2 compared with Bangar *et al.* (2020) who reported only direct effects for ADG and KR traits.
- (4) Direct heritability estimates for ADG_1 and KR_1 under our study were low in magnitude, and may be more precise due to the large sample size.

Correlation estimates

The range for genetic and phenotypic correlations was in accordance with that reported in the published literature by Ghafouri-Kesbi *et al.* (2011) in Zandi, Savar-Sofla *et al.* (2011) in Moghani, Mokhtari *et al.* (2012) in Arman and Ghafouri-Kesbi (2013) in Mehraban sheep. With advancement of age, estimates of genetic correlation usually decrease, but this trend was not perceived in our investigation. Similar findings were reported by Abegaz *et al.* (2005), Ghafouri-Kesbi *et al.* (2011) and Illa *et al.* (2019) in Horro, Zandi and Nellore sheep breeds, respectively. Results for phenotypic correlation were in accordance with findings of Mandal *et al.* (2015) in Muzaffarnagari sheep and Illa *et al.* (2019) in Nellore sheep.

In conclusion, we performed an evaluation of animal models that indicated the potential for direct and maternal effects on growth rate and KR in Harnali sheep. Direct effects were of a low range in magnitude for ADG and KR and indicated the unsuitability of these traits for inclusion in the selection programme. However, maternal effects showed significance for early growth rates and KR, and could be considered to improve the growth efficiency of lambs. It was also suggested that the inclusion of ADG and KR under a breeding plan could markedly diminish unneeded expenditure.

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