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Bayesian estimation of genetic parameters and maternal effects for body weight, average daily gain and Kleiber ratio in Chokla sheep

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Abstract

The present study aimed to investigate genetic parameters and maternal effects for growth performance and feed efficiency traits in Chokla sheep. The dataset comprised 6,785 growth records of Chokla sheep progeny of 499 sires, collected over a period of 47 years (1974–2020) from history-cum-pedigree sheets and databases maintained at the Arid Region Campus of the Central Sheep and Wool Research Institute, Bikaner. Six animal models incorporating different combinations of direct and maternal genetic effects were evaluated to identify the most appropriate model for estimating genetic parameters using Gibbs sampling under a Bayesian framework. Bivariate animal model analysis was performed for estimating correlations based on the best-fitting single-trait models. Traits studied included body weights at birth (BW), 3 (WW), 6 (6W), 9 (9W) and 12 months (YW), along with average daily gain (ADG) and Kleiber ratio (KR) during 0–3 (ADG1/KR1), 3–6 (ADG2/KR2) and 6–12 months (ADG3/KR3). Environmental factors such as period of birth, sex of lamb, season of birth and dam's weight at lambing significantly influenced most traits, except season of birth on 9W and dam's weight at lambing on post-weaning ADGs. Based on the deviance information criterion (DIC), the most suitable model was identified. Posterior mean heritability estimates were moderate for most body weight traits (0.381–0.408), except BW (0.151) and WW (0.134). ADG2 showed the highest heritability among ADGs. Maternal genetic effects were highest for birth weight and declined with advancing age. Negative covariance between direct and maternal effects resulted in inflated additive heritability estimates; therefore, total heritability was considered more appropriate for selection response. Genetic correlations among body weights were positive and moderate to high, indicating six-month body weight as a key selection criterion under field conditions.

Introduction

India is one of the few countries that has made a substantial contribution to the global livestock gene pool. The distribution of livestock resources in the country is relatively more equitable than that of land, making livestock an important component of livelihood security and poverty alleviation programmes. In this context, small ruminants play a crucial role by providing protein-rich food, supplementing farm income, generating rural employment, and contributing to soil fertility.

Growth performance of lambs is a key trait in genetic improvement programmes for sheep. Average daily gain (ADG) is an important determinant of body weight, while the Kleiber ratio (KR) has been recognised as a useful indicator of growth efficiency (Eskandarinasab et al., 2010). For achieving higher growth rates, feed conversion efficiency is considered a more effective selection criterion than body weight alone. Genetic improvement in livestock can be achieved primarily through selection and mating strategies (Falconer, 2009).An effective selection programme requires knowledge of genetic correlations among traits, as these traits are biologically interrelated and selection for one trait may influence others, either positively or negatively. It is well established that additive genetic, maternal genetic, and maternal permanent environmental effects influence the expression of growth traits and contribute to phenotypic variation. Therefore, the formulation of efficient breeding programmes depends on accurate estimation of genetic parameters, which in turn requires precise estimates of (co)variance components after

accounting for relevant non-genetic factors. Improvement in growth performance through selection remains a key strategy for enhancing meat production in lambs (Gholizadeh and Ghafouri-Kesbi, 2015).

Understanding and accurate determination of reliable genetic parameters is crucial for improving breeding efficiency and genetic progress in livestock and poultry populations. These genetic parameters are helpful not only for assessing the breeding value of various traits in livestock and poultry but also for optimizing breeding programs, predicting selection outcomes, and elucidating the genetic mechanisms underlying quantitative traits (Wellmann and Bennewitz, 2019). There are several commonly used methods for estimating genetic parameters and conducting genetic evaluations. These methods include best linear unbiased prediction (Mrode and Thompson, 2005), marker-assisted selection (van Berloo and Stam, 1998), and genomic best linear unbiased prediction (Clark and van der Werf, 2013), AIREML (Thompson et al., 2005; Madsen and Jensen, 2010), Gibbs sampling (Geman and Geman, 1984), BLUPF90 DairyPAK, Version3 (Duanjinda et al., 2007). Among these genetic evaluation methods, the BLUPf90 is the most widely used.

An animal model like AIREML/DFREML takes into accounts all relationship in the pedigree and is therefore expected to provide estimates of genetic parameters with higher precision. Due to extended period of maternal dependence in mammals including livestock species, the early growth traits are not controlled only by direct additive genetic effects but also by maternal effects (Ghafouri-Kesbi and Eskandarinasab, 2008; Maghsoudi *et al.*, 2009). Maternal effects have been defined as any influence from a dam on its offspring, excluding the effects of directly transmitted genes that affect performance of the offspring. Biological mechanisms to explain maternal effects include cytoplasmic inheritance, intrauterine and postpartum nutrition provided by the dam, antibodies and pathogens transmitted from dam to offspring and maternal behavior in multiparous animals, 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. In species having several progenies per parturition, progenies (full sibs) share a common environment that contributes to the likeness among them, which is a further source of variation among families (Falconer and Mackay, 1996). This resemblance refers to some common factors such as nutrition, maternal common care and climatic or nest conditions. Studies on growth traits have shown that including permanent maternal environmental effect in animal models, significantly affected the estimates of direct heritability (h2), even in some studies the proportion of permanent maternal environmental effect to phenotypic variance (c2) was higher than direct and maternal heritabilities (e.g. Ekiz, 2005). when maternal genetic effect is 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. Including maternal effects reduces the bias of genetic parameters estimation (Nasholm and Danell 1994; Gowane et al., 2014; McAdam et al., 2014sänen and Kruuk, 2007). Thus, both direct and maternal components must be considered in order to achieve optimum genetic progress especially in growth traits.

The majority of studies on genetic trait evaluation have employed mixed models under the assumption of a Gaussian distribution. The zero-inflated models have been indicated for analysis of several traits in

different livestock species (Naya *et al.*,2008 and Sae-Lim *et al.*,2017). In these models, it is assumed that the data come from two different distributions: the first one, in which only zeros are generated under a given probability (widely from Binomial distribution); and the second one, in which the data are obtained from a discrete sampling distribution, such as Poisson (Naya *et al.*,2008; Varona and Sorensen, 2010). Although some authors have suggested the use of different models to evaluate discrete and zero-inflated traits (Varona and Sorensen, 2010), there are no reports about using Poisson model for genetic evaluation under a mixed model framework. Given the complexity of count mixed models assuming nonnormal distributions, the Bayesian inference highlights as a practical and efficient statistical tool (Naya et al., 2008; Sorensen, 2009). Bayesian inference, in particular Gibbs sampling (Geman and Geman, 1984), would be an alternative for estimating variance components. Carneiro *et al.* (2007) found that the Bayesian methodology is well justifiable for analyzing small populations or data set when large historical information is attainable. The Gibbs sampling algorithm provided a solution for the problem of limited sample size and produces posterior distributions of parameters to permit random sample estimation of parameter estimates based on a specific data set (Magnabosco *et al.*,2000; Hossein-Zadeh, 2015 and Boujenane and Diallo, 2017).The Bayesian approach has several practical advantages over the classical (REML) approach (Pretorius and Van der Merwe, 2000) like the estimates from the Bayesian approach for a variance are always positive and an interval estimate such as a highest posterior density region will not include negative value.

Several 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 and efficiency traits in small ruminants viz. in various breeds of sheep by Taghi et al. (2016) in Zandi, Nabavi et al. (2014) in Ghezel, Gowane et al. (2015) in Malpura, Mandal et al. (2015) in Muzaffarnagari, Ali et al. (2020) in Kajli lambs, Bakhshalizadeh et al. (2016) in Moghani, Balasundaram et al. (2023) in Mecheri, Gad (2014) in Barki lambs, Gan and Cheng (2022), Ghaderi–Zefrehei et al. (2021) in Lori Bakhtiari, Illa et al. (2019) in Nellore, Illa et al. (2024) in Nellore, Latifi and Mohammadi (2018) in Iranian Afshari ; in various breeds of goat by Gowane et al. (2011) in Sirohi, Gul et al. (2023) in Kilis, Singh et al. (2022) in Barbari and Dige et al. (2021) in Jamunapari.

In the Chokla sheep, estimations of various genetic parameters, genetic and phenotypic correlations for growth performance, daily gain and kleiber ratio have still not been investigated by gibb sampling to date. The main objective of the study was to estimate genetic parameters and maternal for growth traits and feed efficiency traits using gibb sampling by bayesian approach, as well as to obtain genetic and phenotypic correlations between these traits in order to formulate future selection plans for better response to selection for higher growth.

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Material and Methods

Description of data structure

The data belonging 459 sires and 2102 dams used in the present study was collected over a period of 47 years (1974–2020) with 67860 observations from the database of Chokla sheep, maintained at Arid Region Campus of Central Sheep and Wool Research Institute, Dist. Bikaner, Rajasthan.

Classifications of data

The data were classified according to period into eleven periods; season into spring and autumn and sex of lamb 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 on birth weight (BW), weaning weight (WW), six-month body weight (6W), nine-month body weight (9W), twelve-month body weight (YW) and Average daily gain and kleiber ratio at different age interval as 0–3(ADG1/KR1), 3–6 (ADG2/KR2) and 6–12 months (ADG3/KR3) with software **SPSS VERSION 26.0 (2005).** The model was as follows:

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

Where, Where, Y_{ijklm} = Growth performance record of the m^{th} progeny of i^{th} sire born in j^{th} period, k^{th} season belonging to l^{th} sex ;μ = overall mean; S_i = random effect of i^{th} sire; A_j = fixed effect of j^{th} period of birth (j = 1, 2, 3 ...11); B_k = fixed effect of k^{th} season of birth (k = 1, 2); C_l = fixed effect of l^{th} 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, σ^2)

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

Manual for **BLUPF90** family programs by Misztal et al. (2018) was used to estimate bayes estimates for various covariance components in present study. The data were renumbered and processed using **RENUMF90**. The Gibbs sampler was used to obtain posterior densities of (co)variance components. The marginal posterior distribution for each parameter was obtained by integration of multivariate density

functions, considering one long chain with 1, 00,000 iterations. The first 10,000 samples were discarded as burn in and then one out of 200 iterations were used to retain sampled values that reduced lag correlation among thinned samples. The convergence of Gibbs chains was monitored through graphical inspection (trace-plots) related to selected parameters. After verifying the graphics, we observed that the burn-in period considered was sufficient to reach convergence in all parameter estimates. Four hundred fifty (450) number of effective samples were generated and used to obtain measures of central tendency and the HPD region for each parameter. The Geweke diagnostics values of the chain generated by the Gibbs sampler was subjected to **POSTGIBBSF90** (Misztal et al., 2018), were used to check the convergence of genetic analysis. Result could be converged if this is < 1.0 (according to the official manual). The HPD region provides the interval that includes 95% of samples i.e. close idea to 95% confidence interval in frequentist approach and is a measure of reliability. Also, the HPD can be applied to non-symmetric distributions. MCE, corresponding to the “standard error” of the posterior mean of a parameter (μ^-μ). Only significant effects (P ≤ 0.05) were included in the models.

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) = $A\sigma_{am}$ Model 3

$Y = Xb + Z_1a + Z_2m + Wc + \varepsilon$ 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×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.

The total heritability (h^2_t), additive direct heritability (h^2), maternal heritability (m^2) and permanent environmental effects (c^2) were calculated using the following formula:

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

$h^2 = \sigma^2_a / \sigma^2 p$

$m^2 = \sigma^2_m / \sigma^2 p$

$c^2 = \sigma^2_c / \sigma^2 p$

$\sigma^2_p = \sigma^2_a + \sigma^2_m + \sigma^2_c + \sigma^2_e$

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

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

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

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

Goodness of fit for the models was examined using DIC values as:

DIC values are calculated using the samples stored after burn-in. The model giving the lowest DIC value is chosen as the best approximating model for a trait (Nabavi et al., 2014).

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

One of the primary objectives of genetic evaluation is to appropriately partition the genetic variance into direct and maternal components, wherever relevant. The findings of the present study emphasised the importance of selecting an appropriate model for accurate estimation of (co)variance components and genetic parameters for growth traits in Chokla sheep. For subsequent Bayesian analysis, only significant factors identified through preliminary analysis were considered. The analysis of variance indicated that period of lambing, season of lambing, and sex of lamb exerted highly significant ($P \leq 0.01$) effects on all growth traits, except for the effect of season of lambing on body weight at 9 months. Inclusion of ewe's weight at lambing as a covariate in the model significantly ($P < 0.01$) influenced all traits, except post-weaning average daily gains.

(Co) variance components and genetic parameter estimates by appropriate models

The Bayesian Output Analysis package was used to estimate marginal posterior distributions for each (co)variance component and genetic parameter, expressed in terms of mean, median, mode, standard deviation (SD), and 95% highest posterior density (HPD) intervals for all traits. The comparison of mean, median, and mode provided insight into the distribution of variance components and genetic parameters; minimal differences among these measures indicated a near-normal posterior distribution.

Based on the deviance information criterion (DIC), Model 6, which included direct additive genetic effects, maternal additive genetic effects, maternal permanent environmental effects, and covariance between direct additive effects of the animal and dam, was identified as the most appropriate model for 9W, YW, ADG1, ADG3, and KR1. Since pre-weaning growth and feed efficiency traits are strongly influenced by maternal genetic and environmental effects, Model 6 was considered most suitable for these traits.

For other traits, including BW, 6W, ADG2, KR2, and KR3, Model 3, incorporating direct additive and maternal genetic effects along with their covariance, showed the best fit based on DIC values. The influence of maternal permanent environmental effects declined after weaning as animals became more independent, which explains the suitability of Model 3 for post-weaning traits. For weaning weight (WW), Model 5, which included direct additive, maternal genetic, and maternal permanent environmental effects with zero covariance between direct and maternal effects, was found to be the best-fitting model in the present study. This observation differs from earlier reports, where different models were identified as optimal: Taghi et al. (2016) reported Model 5 for BW, Model 4 for WW, Model 6 for 6W, and Model 5 for 9W in Zandi sheep; Balsundaram et al. (2023) reported Model 2 for all age groups in Mecheri sheep; Ghaderi–Zefrehei et al. (2021) reported Model 2 for BW and WW, Model 6 for 6W and YW, and Model 5 for 9W in Lori Bakhtairi sheep; Kushwaha et al. (2009) reported Model 5 for BW, Model 3 for WW, 9W, and YW, and Model 2 for 6W in Chokla sheep; and Prince et al. (2010) reported Model 1 for BW and ADG3 and Model 4 for WW, 6W, 9W, YW, ADG1, and ADG2 in Avikalin sheep.

Posterior mean, median and mode of various variance genetic parameters and heritability by best model for body weights, ADGs and KRs were summarized in Tables 1, 2 and 3, respectively. Results showed that posterior mean, median and mode for all genetic parameters and heritability for all models were found approximate equal. So, it may be concluded that normal distribution was existed for estimated bayes estimates by gibb sampling for genetic parameters and heritability for all studied traits in present study.

An incremental increase in additive heritability values for the body weight traits was found according to the age of the animal except for weaning weight (Table 1 and Fig. 1). Decrease of this heritability from birth to weaning stage may be possible due to inclusion of maternal effect at weaning stage. The posterior mean of h^2 values for all the body weight traits except BW (0.151) and WW (0.134) were

moderate (0.381–0.408). Lower heritability of birth weight compared to the other weights because of fetal growth is influenced by genetic and environmental factors such as the placenta and the fetal nutrition by a dam. Therefore, environmental factors affecting dam growth, especially the quality and quantity of food and the storage of food for dam can influence the growth of the embryo. The direct heritability estimates for ADGs and KRs showed same pattern of variation as both show increase in stage 3 to 6 months (ADG2/KR2) and both decreases afterwards (ADG3/KR3) as shown in Fig. 1. The most heritable trait among body weights was nine months body weight (0.408) and among feed efficiency traits ADG2 (0.376). So, post weaning live weights and daily gains were moderate to high, indicating further scope of genetic improvement through selection in these traits.

Direct heritability for BW is close agreement with Mandal et al. (2015) in Muzaffarnagri as. 0.15 and for WW with finding of Matika et al. (2003) in Sabi sheep. Whereas, Latifı and Mohammadi (2018) in Iranian Afshari found lower estimate for WW as 0.05. Posterior mean of additive heritability for BW, 6W and YW was higher than estimates of Gowane et al. (2015) in Malpura and Ill et al. (2020) in Nellore sheep, Hossein-Zadeh (2012) in Moghani, Ali et al. (2020) in Kajli sheep Bahreini Behzadi et al. (2007) in Kermani, while lower than Matika et al. (2003) in Sabi, Balsundaram *et al.* (2023) in Mecheri, Hanford et al. (2005) in Rambouillet sheep. While, additive heritability of WW was lower than estimates obtained by Gowane et al. (2015) as 0.40 in Malpura, Taghi et al. (2016) as 0.169 in Zandi, Mandal et al. (2006) in Muzaffarnagri as 0.21, Mandal et al. (2015) in Muzaffarnagri as 0.16 and Ill et al. (2020) in Nellore sheep as 0.28. The posterior mean of h^2 of 9W was found in close agreement with the findings of Gownae *et al.* (2015) as 0.37 in Malpura sheep. Gad *et al.* (2014) in barki lambs for YW estimated lower heritability than present study as 0.10. Ghaderi–Zefrehei et al. (2021) in Lori Bakhtairi reported higher for BW and WW as 0.36, 0.18, and lower for 6W, 9W and YW as 0.21, 0.27, 0.32. Kushwaha et al. (2009) in Chokla higher for BW, WW as 0.20, 0.18 lower for 6W, 9W and YW as 0.16, 0.22, 0,23; Additive direct heritability estimates for ADGs and KRs was higher than the earlier estimate by Gowane et al. (2015) in Chokla sheep, Mandal et al. (2015) in Muzaffarnagri, Matika et al. (2003) in Sabi. Lower estimates of additive direct heritability were reported by Matika et al. (2003) in Sabi, Hossein-Zadeh (2012) in Moghani, Abbasi *et al.* (2011) in Makooei for YW and higher by Illa et al. (2024) in Nellore as 0.11. Prince et al. (2010) in Avikalin higher for BW, WW lower than present 6W, 9W, YW, ADG1, ADG2, ADG3.Lower estimates of direct heritability were reported by Mohammadi et al. (2010) as 0.15 in Sanjabi; Prakash et al. (2012) as 0.20 in Malpura for KR1. Illa et al. (2019) in Nellore reported higher estimates for ADGs and KRs for ADG1 ADG2 KR1 KR2 as 0.37, 0.41, 0.34, 0.48. Similarly, lower estimate of h^2 for KR2 were reported by Mohammadi et al. (2010) as 0.07 in Sanjabi, Ghafouri-kesbi et al. (2011) as 0.06 in Zandi sheep and for KR3 by Ghafouri-kesbi et al. (2011) as 0.10 in Zandi, Prakash et al. (2012) as 0.23 in Malpura sheep. lower estimates of direct heritability obtained by Boujenane and Kansari (2002) as 0.05 for BW, 0.06 for WW in Timahdite; Mandal et al. (2006) in Muzaffarnagri as 0.09 for BW, 0.06 for 6W, 0.10 for 9W, 0.14 for YW. Additive heritability estimate for PWDG was higher than present by Latifı and Mohammadi (2018) in Iranian Afshari. Qin et al. (2024) estimated heritability as 0.12 for body weight in ujumqin sheep which is lower than present.

The maternal genetic effect (m^2) was found to be highest at birth weight (0.286). In these data, the maternal influence diminished as age increases (Table 1 and Fig. 1). In present study noticeable decrease in maternal effect from birth to weaning as 0.286 to 0.039 was found. This is due to estimated fitted model in which additive and maternal effect with zero covariance. At six-month, posterior mean of maternal effects (m^2) was estimated as 0.112, which was reduced from birth. At six months stage, due to similar plane of nutrition for all the individuals in the flock, reduced the environmental variability resulting in higher heritability values. Therefore, weight at six months can be considered a good criterion for selection animals. Maternal effect was fluctuating in similar manner for ADGs and KRs as decreased from pre weaning to first post weaning stage at 3 to 6 months of age. For preweaning ADG1 and KR1 m2 estimates were 0.133, 0.113, which was further decreases as 0.099 and 0.111 for ADG2 and KR2, as shown in Fig. 1. Thus, for ADG2 and ADG3, maternal effects had lesser role to play as compare to ADG1 for determining growth rate. Posterior mean of maternal effect (m2) for corresponding KRs was estimated as 0.113, 0.111 and 0.123, respectively. It may be concluded that slightly higher maternal effect was reported on KR3 as compared to KR1 and KR2. Although decreasing pattern was found in ADG2 as compare to KR2. It is due to after weaning stage maternal effect start to decreases.

The result indicates that maternal additive genetic effects, which regard to the growth of fetus, could have some beneficial effect on the post-natal growth traits too. The low estimates of maternal heritability for 6W and 9W were expected, because at these ages individuals do not depend on their mother and their weights should reflect only the direct effect of the genes on growth except for carry over maternal effects from before weaning. For animals raised on pasture, the length of time from birth to yearling is probably not enough that compensatory gain could buffer completely the maternal effect existing at birth. Robison (1981) suggested that even if maternal effects tend to diminish with age, some adult traits will nevertheless contain this source of variation. In general, different estimates of the direct and maternal heritability of body weight traits in various studies can be due to model of analysis, sheep breed, data structure, different management of herds and different breeding strategies in sheep. The relatively low heritability estimates for the studied traits can be perhaps explained by the low nutritional management, low quality of pastures and harsh climatic conditions, which result in a high environmental variance. Sizeable effects of maternal influences on BW and pre weaning ADG/KR suggest that these effects need to be considered in selection programs and exclusion of them may lead to biased estimations of direct heritability. When maternal effects are of high importance, total heritability values are more efficient than direct heritability for estimation of selection response based on phenotypic values.

Although maternal effects cannot be compared with the other studies due to differences in the models fitted, as suggested by Meyer (1992). Similar to present result Matika et al. (2003) in Sabi, Balsundaram *et al.* (2023) in Mecheri, Bahreini Behzadi et al. (2007) in Kermani, Mandal *et al.* (2009) in Muzaffarnagari, Ghaderi–Zefrehei et al. (2021) in Lori Bakhtairi, Hanford et al. (2005) in Rambouillet, Kushwaha et al. (2009) in Chokla and Prince et al. (2010) in Avikalin observed maternal heritability declined from birth to 60 days of age and was negligible thereafter. Contrary to this Hossein-Zadeh (2012) estimated

increasing pattern from BW to WW as 0.16, 0.42 in Moghani sheep. Maternal genetic effects contributed only 12% of the total variance for birth weight according to Mandal et al. (2015) in Muzaffarnagri; However, Lower maternal heritability for BW,6W, 9W and YW were reported by Gowane et al. (2015) as 0.23;0.21;0.21 in Malpura and Ill et al. (2020) as 0.12;0.14;0.12 in Nellore sheep, Boujenane and Kansari (2002) in Timahdite, Balsundaram *et al.* (2023) in Mecheri, Ghaderi–Zefrehei et al. (2021) in Lori Bakhtairi, Latifi and Mohammadi (2018) in Iranian Afshari than present result, respectively. While, higher estimates of maternal heritability for WW as 0.15, 0.071 and 0.14 than present study were obtained by Gowane et al. (2015) in Malpura, Taghi et al. (2016) in Zandi and Ill et al. (2020) in Nellore sheep, respectively. The maternal heritability of YW was in close agreement with estimate of Ill et al. (2020) as 0.13 in Nellore and Gad *et al.* (2014) in barki lambs as 0.12. Illa et al. (2024) in Nellore estimated lower maternal effect for YW as 0.09. Higher estimate of maternal heritability was reported by Gowane et al. (2015) as 0.16 for ADG1 and 0.22 for ADG2 in Malpura sheep. Higher estimates for 6W, 9W, YW than present were reported by Bahreini Behzadi et al. (2007) in Kermani. Kushwaha et al. (2009) in Chokla estimated lower maternal effect for all body weight traits than present study. Qin et al. (2024) estimated maternal heritability as 0.35 for body weight in ujumqin sheep which is higher the present finding. Results suggested scope of further genetic improvement in post-weaning weights by selection.

According to results of Bayesian approach results, maternal permanent environmental effect (c^2) was found to influence the weaning weight (0.023) and pre weaning average daily gain (0.017). Other traits which were influenced minor by maternal permanent environment effect were 9W (0.003), YW (0.014), ADG3 (0.006) and KR1 (0.010). Maternal permanent environmental effect was negligible or nearly absent in the post weaning traits as well as at birth weight stage and indicated the importance of impact of animal's own genotype for body weight at the time of birth and after post weaning stage it is estimated minor. However, Tosh and Kemp (1994) observed that the permanent environmental effect consistently decreased in importance as lambs became increasingly independent of the ewe. Boujenane and Kansari (2002) estimated 0.00 for BW,0.03 for WW in Timadhite which is close agreement with present result. Mandal et al. (2015) in Muzaffarnagri estimates of fraction of variance due to maternal permanent environmental effects (c2) for BW, WW, ADG and KR accounted for 6–12% of the total phenotypic variance in their study which is higher to present study. Similarly, Ghaderi–Zefrehei et al. (2021) in Lori Bakhtairi reported higher environmental effect as 0.14, 0.11, 0.02, 0.02, 0.008 for BW, WW, 6W, 9W, YW. Hanford et al. (2005) in Rambouillet reported environmental effect for birth (0.07) and weaning stage (0.04). higher environmental effect for YW was observed by Illa et al. (2024) in Nellore as 0.06. Kushwaha et al. (2009) in Chokla reported observable environmental effect for BW, 6W as 0.12, 0.08, respectively. Prince et al. (2010) in Avikalin observed negligible environmental effect as similar to present study for WW, 6W, 9W, YW, ADG1, ADG2 as 0.03, 0.03, 0.04, 0.01, 0.00.

The repeatability of ewe performance was largest at birth and then gradually declined at more advanced ages for body weights and ADG/KR. The various estimates of tm reflect the overall repeatability of ewe performance and as such are both relatively accurately determined in data sets of this size and, so long as maternal effects are included in the model, are relatively robust to the model actually fitted. In

contrast, partition of the overall ewe effect into its components (h^2, m^2, c^2 and r_{am}) is much more challenging, requiring repeated records on related ewes. Knowledge of tm is adequate to predict future ewe performance and the phenotypic response to culling, but prediction of genetic responses to selection requires accurate estimates of m^2, h^2 and ram. Similar consistency of tm across models was reported by Notter and Hough (1997), who likewise observed some difficulty in achieving reliable partitioning of tm into its components. Addition of covariance between direct and maternal effects in model 3 and model 6 has shown negative and high estimate of σ_{am}, which resulted in highly inflated values of heritability and maternal effect in these models. So, it is more appropriate 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 direct heritability. The Posterior mean of estimates of t_m and h^2_t were estimated as 0.083and 0.182; 0.154 and 0.095; 0.147 and 0.014; 0.166 and 0.022; 0.143 and 0.026 for BW, WW, 6W, 9W and YW, respectively. Posterior mean of estimates of t_m and h^2_t were found to be 0.046 and 0.107; 0.001 and 0.136; 0.014 and 0.077for ADG1, ADG2 and ADG3, respectively. The ADG2 show least t_m value and highest total heritability among all ADGs. Posterior mean of estimates of t_m and h^2_t were found to be 0.050 and 0.153; .002 and 0.124; 0.011 and 0.096 for KR1, KR2 and KR3, respectively by appropriate models. Thus, KR1 show highest total heritability while, KR2 show least t_m value among all kleiber ratios. The result indicated reasonable scope of improvement in the trait through selection. lower values of h_t^2 in models that included an additive direct–maternal covariance (i.e., Models 5 versus 6). Selection to improve preweaning growth will be less effective if there is genetic antagonism between direct and maternal additive effects. However, accurate estimation of r_{am} has proven difficult (Robinson, 1996). Total heritabilities for postnatal weights were low to moderate in magnitude, ranging from 0.08 to 0.19. Estimates of total heritability for various body weights were within the range of other estimates made at similar ages (Boujenane and Kansari, 2002). Qin et al. 2024 estimated total heritability as 0.29 for body weight in ujumqin sheep which is higher to present result. Boujenane and Kansari (2002) estimated lower estimates of h^2_t as 0.03 for BW,0.06 for WW in Timadhite. Illa et al. (2024) in Nellore for YW as 0.16 is close agreement with result. Kushwaha et al. (2009) estimated higher total heritability in Chokla for BW, WW, 6W, 9W and YW as 0.25, 0.18, 0.16, 0.26, 0.27 and higher tm 0.26, 0.13, 0.12, 0.13, 0.14, respectively. Similarly, Prince et al. (2010) in Avikalin observed higher h2t and tm for all body weights and ADGs and Latifi and Mohammadi (2018) in Iranian Afshari observed little higher estimates of h2t for BW and lower for WW, PWDG. For ADG1 and ADG2, estimates of tm were in congruence with earlier report of Prakash et al. (2012).

Bayesian approach gives more precise estimates of maternal effect and permanent maternal effect for early expressed growth trait as compared to WOMBAT and shown in reliability study conducted by Choudhary et al., 2022.

Genetic, maternal permanent environment and maternal Correlations estimate

Estimates of direct genetic, maternal genetic and permanent environmental correlations for body weights are presented in Table 4, while those for feed efficiency traits (ADGs and KRs) are summarized in Table 5. Genetic correlations among body weights at different ages were generally positive and ranged from medium to high, except for BW–WW (–0.540) and BW–9W (–0.076) (Table 4). For direct genetic correlations among live weights, a low estimate (0.066) was observed for BW–YW, whereas the highest estimate was recorded for 9W–YW (0.829). Positive genetic associations were observed between WW and 6W, and between 6W with 9W and YW, suggesting that body weight at the weaning stage may be considered an important criterion for improving body weight at later ages. High genetic correlations among body weight traits indicate that similar genetic factors influence body weight from weaning to adulthood. These findings are contrary to those reported by Boujenane and Kansari (2002) in Timahdite sheep, who observed negative and low-to-moderate direct–maternal additive genetic cross-correlations. Only a few traits showed environmental correlations, namely WW–9W (0.318), WW–YW (0.269) and 9W–YW (0.441), although these associations were non-significant. This suggests that permanent environmental correlations become more influential at later stages of growth when animals increasingly depend on environmental conditions. Birth weight exhibited a positive maternal correlation with WW (0.186), while later body weights showed negative or negligible maternal associations, indicating that maternal effects are more pronounced up to birth and weaning stages, though non-significant in the present study. Similar or contrasting trends have been reported by Mandal et al. (2015), Ali et al. (2020), Bahreini Behzadi et al. (2007), Balsundram *et al.* (2003), Prakash et al. (2012), Illa et al. (2019), Hanford et al. (2002, 2003) and Gowane et al. (2010).

High, positive and highly significant ($P \leq 0.01$) genetic correlation was found between ADG1-KR1(0.970), ADG2-KR2 (0.956), ADG3-KR3 (0.952) and KR1-KR2(0.668) (Table 5), indicating that selection for one of the ADG should result in genetic improvement in corresponding KR also. Contrary to this, Illa et al. (2019) in Nellore observed negative correlation between ADG1-KR1 (-0.99). Negative genetic correlation between ADG1-ADG2 is as similar to results of Gowane et al. (2015) in Malpura sheep (-0.19). Maternal genetic correlation was found positive, high and significant for corresponding ADGs and KRs. Highest maternal association was found for ADG1-ADG2 (0.998), ADG1-KR1 (0.888) while lowest for ADG1-KR3 (0.026), KR2-KR3(0.058). Environmental correlation was found for few traits as ADG1-ADG3 (-0.43), ADG1-KR1 (0.79), ADG3-KR1 (0.099).

Table 4
Correlation estimates among body weight traits by BLUPF90 software by bivariate analysis

trait	r_g	r_c	r_m
BW-WW	-0.540 (0.479)	-	0.186 (0.313)
BW-6W	0.138(0.289)	-	-0.080(0.208)
BW-9W	-0.076(0.214)	-	-0.213(0.297)
BW-YW	0.066(0.205)	-	0.009(0.153)
WW-6W	0.628**(0.259)	-	-0.060(0.220)
WW-9W	0.421(0.280)	0.318(0.270)	0.073(0.112)
WW-YW	0.389(0.217)	0.269(0.119)	0.061(0.137)
6W-9W	0.653**(0.305)	-	0.324(0.209)
6W-YW	0.571**(0.291)	-	0.487(0.306)
9W-YW	0.829**(0.389)	0.441(0.304)	0.564(0.319)

In bracket PSD was written; r_g- additive genetic correlation, r_m-maternal additive genetic correlation, r_c-maternal permanent environmental correlation and ** - Highly significant ($P \leq 0.01$); * - Significant ($P \leq 0.05$)

Table 5
Correlation estimates among ADGs and KRs by BLUPF90 software by bivariate analysis

Trait	r_g	r_c	r_m
ADG1-ADG2	0.413(0.117)		0.998**(0.441)
ADG1-ADG3	-0.098(0.217)	-0.43634 (0.75)	-0.0198(0.235)
ADG1-KR1	0.970**(0.008)	0.79097 (0.15)	0.888**0.045)
ADG1-KR2	0.227(0.098)		-0.883**(0.451)
ADG1-KR3	-0.0345(0.10)		0.0268(0.141)
ADG2-ADG3	0.673(0.329)		0.807**(0.331)
ADG2-KR1	0.289(0.397)		0.513(0.406)
ADG2-KR2	0.956** (0.009)		0.869**(0.066)
ADG2-KR3	0.30519 (0.182)		0.0786(0.37)
ADG3-KR1	-0.0997(0.288)	0.099(0.121)	-0.907(0.304)
ADG3-KR2	-0.161(0.157)		0.724(0.198)
ADG3-KR3	0.952** (0.011)		0.964**(0.024)
KR1-KR2	0.668*(0.430)		-0.887**(0.178)
KR1-KR3	-0.117(0.119)		-0.914**(0.227)
KR2-KR3	-0.193(0.34)		0.0584(0.21)
Footnote same as Table 4			

Conclusion

The study revealed that the moderate heritability in economically important traits indicates that modest rates of genetic progress may be possible for these traits from selection under the prevailing management system. The six-month body weight showed high and positive phenotypic correlation with 9- and 12-months body weight, this indicated that a lamb weighed heavier at 6 months of age, was likely to be heavier at 9 and 12 months of age. In the field conditions, generally six months body weight is market age to sale and purchase of animals, this trait would be important criteria for evaluation of lambs in field conditions. Results indicated that maternal effects decreased as age advanced, while moderate genetic improvement remained achievable for all pre-weaning growth traits evaluated in Chokla sheep. Thus, enhancement of post-weaning growth performance should emphasize the refinement of non-genetic factors, particularly management, nutrition, and environmental conditions, alongside indirect selection strategies employing genetically correlated, highly heritable traits.

Declarations

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Conflict of interest - The authors have no conflicts of interest to declare that are relevant to the content of this article.

Ethics approval – No approval of research ethics committees was required to accomplish the objective of this study because the manuscript does not contain clinical studies or patient data.

Data availability statement – data will be made available from corresponding author on reasonable request/requirement.

Authors' contribution – All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by all authors. The first draft of the manuscript written and prepared by Garima Choudhary. All authors read and approved the final manuscript.

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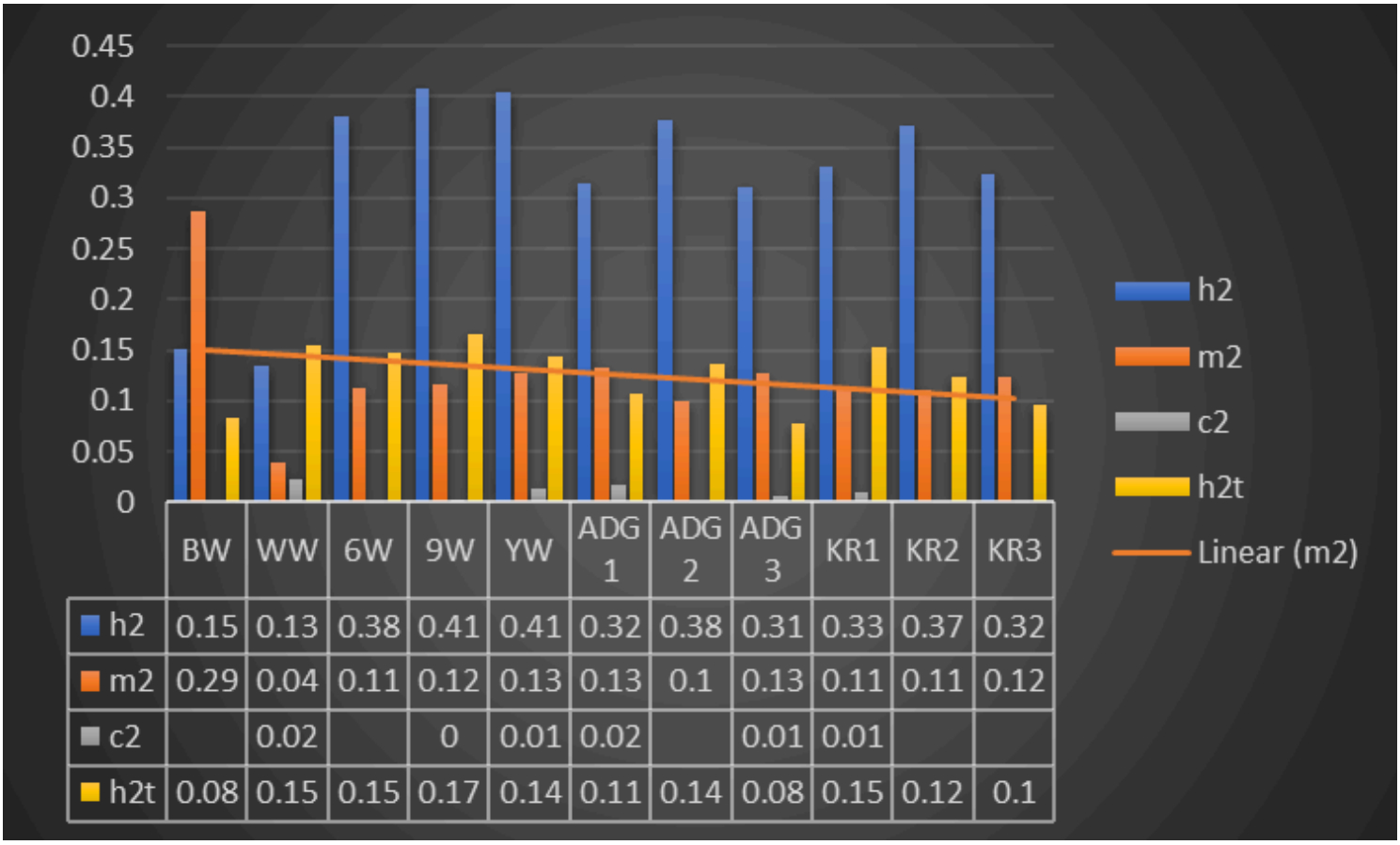
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Table 1 To 3

Table 1 To 3 are available in the Supplementary Files section.

Figures



	BW	WW	6W	9W	YW	ADG 1	ADG 2	ADG 3	KR1	KR2	KR3
h2	0.15	0.13	0.38	0.41	0.41	0.32	0.38	0.31	0.33	0.37	0.32
m2	0.29	0.04	0.11	0.12	0.13	0.13	0.1	0.13	0.11	0.11	0.12
c2		0.02		0	0.01	0.02		0.01	0.01		
h2t	0.08	0.15	0.15	0.17	0.14	0.11	0.14	0.08	0.15	0.12	0.1

Figure 1

estimates of additive, maternal, environmental and total heritability of various studied traits

Supplementary Files

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- Table1to3.docx