RESEARCH ARTICLE

Estimates of (Co)-Variance Components and Genetic Parameters for Growth Efficiency Traits by Animal Model in Chokla Sheep

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ABSTRACT

This study obtained genetic data from pedigree records of Chokla lambs over 47 years (1974-2020) and 6785 records of performance were available at Central Sheep and Wool Research Institute, Bikaner, Rajasthan, India. (Co)variance components and genetic parameters of average daily gain and Kleiber ratio were estimated by average algorithm restricted maximum likelihood (AIREML), fitting six different animal models with various combinations of direct and maternal effects. Direct heritability estimates were inflated substantially for all traits when maternal effects were ignored. The direct additive heritability h^2 values for all ADGs and KRs were moderate (0.3-0.4). The maternal influence diminished as age increased and found to be important and sizeable at pre-weaning stage. Negative and high estimate of covariance between direct and maternal effects, resulted highly inflated values of additive heritability. To avoid using skewed estimates of additive heredity in this situation, it is more beneficial to evaluate the response for selection based on phenotypic values using total heritability (h^2_t). If lambs are chosen for greater feed efficiency based on KR, there may be scope for indirect selection for growth rate, according to positive correlations shown between ADG and KR.

Key words: Chokla, Correlation, (Co)-Variance components, Genetic parameters, Maternal effect.

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INTRODUCTION

Growth potential of the lambs is one of the most important traits in a genetic improvement scheme for sheep. The Kleiber ratio is a measurement for efficiency, independent of body size (Kleiber, 1961). It was indicated by Scholtz *et al.* (1990) that the Kleiber ratio, expressed as post-weaning ADG/(mature mass)$^{0.75}$ could be used as an indirect selection parameter for feed conversion. 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. To improve the growth and production there are mainly two tools in the hand of animal breeders *i.e.* either by selection or mating (Falconer, 2009). 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. Improving growth performance by selection programs is an important method to increase meat production in lamb breeding herds (Gholizadeh and Ghafouri-Kesbi, 2015). Sheep has high potentials of growth and reproduction and adapt to cold climate and must be considered in breeding program (Hossein-Zadeh, 2012).

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. 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 (Ghafouri-Kesbi and Eskandarinasab, 2008; Maghsoudi *et al.*, 2009). Maternal

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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, 2009). 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 common environmental effect in animal models, significantly affected the estimates of direct heritability (h^2), even in some studies the proportion of common environmental effect to phenotypic variance (c^2) was higher than direct and maternal heritabilities (Ekiz, 2005). Nasholm and Danell (1994) observed that when maternal genetic effect 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 including maternal effects reduces the bias of genetic parameters estimation. 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; Mahala *et al.,* 2020). Hence, present study was undertaken to estimate various (co)variance components and genetic parameters for Average daily gain and Kleiber ratio at different age interval in sheep.

MATERIALS AND METHODS

Source and Classifications of Data

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 (Rajasthan, India) were collected over a period of 47 years (1974 to 2020). The data were classified according to period into eleven periods/groups; season into spring and autumn and sex of lamb into male and female group.

Statistical Analyses

The data were analysed to examine the effects of period, season, sex and ewe weight at lambing on Average daily gain (ADG) 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 ADG in g/day was calculated as ADG = (yt2 - yt1) / ($t_2 - t_1$)

Where, y_{t1} and y_{t2} refer to body weights at t_1 and t_2 ages in days respectively (Fitzhugh and Taylor, 1971).

Kleiber ratio (KR) is the proportion of ADG to the metabolic body weight and this ratio was calculated as KR = $ADG/W^{0.75}$

Where, ADG = Average daily gain for the period expressed in g/day, and $W^{0.75}$ = Metabolic body weight at the older age of the period for which KR is calculated

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 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.

(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.

Various animal models by ignoring or including various combinations of maternal genetic and permanent environmental effects were fitted to estimate genetic parameters for each trait. In model 1 additive effect; in model 2 additive and maternal effect with zero covariance between both effect, model 3 same as model 2 but having non-zero covariance between additive and maternal effect, model 4 additive and maternal permanent environmental effect, model 5 additive, maternal, maternal permanent environment effect with zero covariance between additive and maternal effect and model 6 is same as model 5 but there is non-zero covariance between additive and maternal effect, were fitted to estimate maternal effect and covariance components.

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

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.

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

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

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

The direct-maternal correlation (r_{am}) 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 likelihood based criteria as:

$AIC = -2Log\ L_i + 2p_i$ (Akaike, 1983)

Where log $\mathbf{L_i}$ is the maximized log likelihood of model **i** at convergence and $\mathbf{p_i}$ is the 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 (Maniatis and Pollott, 2003). Descriptive statistics were summarized for ADGs and KRs at different age intervals in Table 1.

According to present study all non-genetic factors like period of lambing, season of lambing, sex of lamb and ewe's weight at lambing had highly significant ($p<0.01$) effect on all traits, except ewe's weight on ADG2 and ADG3.

(Co)Variance Components and Genetic Parameter Estimates

Estimates of phenotypic variance using the different models were found generally similar for all the traits studied and

Table 1: Descriptive statistics and data structure for ADG and KR using animal model in Chokla sheep

Trait		ADG1/KR1 (0-3 months)	ADG2/KR2 (3-6 months)	ADG3/KR3 (6-12 months)
Mean	ADG (gm/day)	118.70	64.95	30.61
	KR	16.43	6.80	2.71
Standard error	ADG	0.550	0.700	0.490
	KR	0.033	0.056	0.038
Minimum	ADG (gm/day)	30.00	15.56	10.00
	KR	6.90	1.47	0.67
Standard deviation	ADG	36.70	33.573	15.495
	KR	2.080	2.561	1.111
Maximum	ADG (gm/day)	270.00	206.67	117.78
	KR	22.26	16.42	8.33
CV%	ADG	30.91	51.69	50.60
	KR	12.65	37.66	40.99
Skewness	ADG	-0.39	0.26	0.54
	KR	-0.50	-1.01	0.85

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

Traits	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}
ADG1	0.377 ±0.048	0.171 ±0.025	-	-0.861 ±0.036	0.134	0.046	318.957	144.853	-	567.52	846.29	-185.042
ADG2	0.457 ±0.047	0.114 ±0.023	-	-1.00 ±0.030	0.171	0.0015	403.257	100.880	-	580.17	882.61	-201.693
ADG3	0.380 ±0.055	0.144 ±0.032	-	-0.982 ±0.035	0.107	0.01	71.256	26.935	-	132.26	187.41	-43.042
KR1	0.388 ±0.050	0.137 ±0.024	-	-0.786 ±0.048	0.184	0.053	1.218	0.429	-	2.058	3.137	-0.569
KR2	0.460 ±0.051	0.129 ±0.025	-	-0.999 ±0.026	0.158	0.004	2.618	0.735	-	3.720	5.687	-1.386
KR3	0.393 ±0.056	0.146 ±0.032	-	-0.980 ±0.035	0.114	0.0096	0.433	0.161	-	0.766	1.101	-0.258

residual variance also approx similar in models 1-6. As per AIC, best model found was model 3 for all ADGs and KRs, which included additive direct effect, maternal effect with non-zero covariance between additive and maternal effect. (Co)variance components and genetic parameters estimated by the best model 3 in univariate analysis by WOMBAT for each trait of Chokla sheep are presented in Table 2.

Additive genetic heritability for ADG1, ADG2, ADG3, KR1, KR2 and KR3 from the most suitable model (model 3) was 0.377±0.048, 0.457±0.047, 0.380±0.055, 0.388±0.050, 0.460±0.051 and 0.393±0.056, respectively. Thus as similar to ADG2, KR2 was also observed highly heritable trait. The higher estimates of h^2 for pre-weaning growth rates found in result indicated the existence of higher genetic variance for these traits and thus the great possibility of selecting the animals for these traits. The better nutritional status and body condition score of the dam at the lambing allowed the minimal impact of maternal effects, which could have masked the additive genetic effect of the animal.

The estimates of additive heritability of pre- and post-weaning average daily gains were reported similar to estimates by Mahala *et al.* (2020) and Gowane *et al.* (2015) for Malpura, Aguirre *et al.* (2016) in Santa Ines sheep, and Lalit *et al.* (2016) in Harnali. Although lower estimates of additive direct heritability for ADGs were reported by Mohammadi *et al.* (2010) in Sanjabi; Prakash *et al.* (2012) in Malpura; Vivekanand (2013) in Magra; and Singh *et al.* (2016) in Marwari sheep. While higher estimates of direct heritability were reported by Gowane *et al.* (2015) in Malpura and Mahala *et al.* (2020) in Avikalin sheep.

Lower estimates of additive direct heritability were reported by Mohammadi *et al.* (2010) in Sanjabi; Prakash *et al.* (2012) in Malpura; Mokhtari *et al.* (2013) in Arman for Kleiber ratio. While higher estimates of heritability were reported by Mahala *et al.* (2020) in Avikalin. Almost equal estimate of additive direct heritability for KR3 was reported by Mahala *et al.* (2020) as 0.39±0.06 in Avikalin sheep.

Maternal effect (m^2) for corresponding traits was estimated (by model 3) as 0.171±0.025, 0.114±0.023 and 0.144±0.032, respectively. For ADG2, maternal effects had lesser role to play as compared to ADG1 and ADG3 for determining growth rate. Maternal effect (m^2) for corresponding KRs was estimated (by model 3) as 0.137±0.024, 0.129±0.025 and 0.146±0.032, respectively. It may be concluded that for KR1 and KR2, maternal effects had lesser role to play as compared to KR3 for determining growth rate. This pattern of result was in agreement with earlier reports by Gowane *et al.* (2015) in Malpura, Gholizadeh and Ghafouri-kesbi (2015) in Baluchi, and Mahala *et al.* (2020) in Avikalin sheep.

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.

Reason behind high and negative r_{am} was found by various researchers (Tosh and Kemp, 1994; Robinson, 1996; Berweger *et al.,* 1999; Notter and Hough, 1997; Roff, 2002). 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 pleiotrophy 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; Berweger *et al.,* 1999). 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.

Estimates of t_m and h^2_t were found to be 0.046 and 0.134; 0.0015 and 0.171; 0.01 and 0.107 for ADG1, ADG2 and ADG3, respectively, while 0.053 and 0.184; 0.004 and 0.158; 0.0096 and 0.114 for KR1, KR2 and KR3, respectively. Traits from weaning to six months (ADG2 and KR2) showed least t_m value, while ADG2 and KR1 showed highest total heritability. The result indicated reasonable scope of improvement in the trait through selection. Similar estimates of total heritability have been reported by Gowane *et al.* (2015) in Malpura and Mahala *et al.* (2020) in Avikalin for pre-weaning ADG; Jaffaroghli *et al.* (2010) in Moghani, Prince *et al.* (2010) in Avikalin and Singh *et al.* (2016) in Marwari for post-weaning ADG.

While Higher estimates were reported by Mohammadi *et al.* (2010) in Sanjabi; Prakash *et al.* (2012) in Malpura; Vivekanand (2013) in Magra; Singh *et al.* (2016) Marwari for pre- weaning ADG, on the contrary lower estimates were reported by Jaffaroghli *et al.* (2010) in Moghani, Gowane *et al.* (2015) in Bharat Merino for ADG1; Abegas *et al.* (2005) in Horro, Mohammadi *et al.* (2010) in Sanjabi, Gowane *et al.* (2015) as 0.045 in Malpura for post-weaning ADG. Slightly higher estimates of total heritability for pre-weaning Kleiber ratio were reported by Prakash *et al.* (2012) in Malpura and Mahala *et al.* (2020) in Avikalin, while lower estimates were reported by Abegas *et al.* (2005) in Horro and Mohammadi *et al.* (2010) in Sanjabi.

Correlations among Body Weight at Different Ages

In condition of indirect selection, correlation study is effective way to select secondary trait. It is practically difficult to measure the individual intake of animals for direct selection of animals for lower maintenance requirements. The Kleiber ratio has been recommended to accomplish this goal (Arthur *et al.,* 2001). The estimates of different correlations among pre- and post-weaning ADG and KR are presented in Table 3.

Table 3: Correlation estimates between ADG and KR under bivariate animal models

Trait	rg	rp	rm	re
ADG1-ADG2	0.356±0.110	-0.006 ±0.016	0.997**	-0.086±0.022
ADG1-ADG3	-0.110±0.132	-0.145±0.019	-1.000*	-0.135±0.026
ADG1-KR1	0.971**±0.009	0.943**±0.002	0.788** ±0.069	0.946**±0.002
ADG2-ADG3	-0.315 ±0.108	-0.287±0.018	0.794**	-0.282±0.025
ADG2-KR2	0.954** ±0.011	0.939**±0.002	-0.943**	0.939**±0.003
ADG3-KR3	0.936**±0.017	0.959** ±0.002	0.159	0.963* ±0.002
KR1-KR2	0.155 ± 0.120	-0.276±0.015	-0.911**	-0.366±0.020
KR1-KR3	-0.337±0.112	-0.303 ±0.018	-0.996** ±0.541	-0.280± 0.025
KR2-KR3	-0.324 ±0.115	-0.284±0.018	0.932**	-0.281±0.024

r_g- additive genetic correlation, r_p-phenotypic correlation, r_m-maternal additive genetic correlation and r_e-residual correlations; ** - Highly significant ($P \leq 0.01$) ; * - Significant ($P \leq 0.05$)

High, positive and statistically significant genetic correlation was found between growth efficiency traits which agreed with the findings of Mahala *et al.* (2020) in Avikalin sheep.

The phenotypic correlations of ADGs with different KR were negative and low to medium in magnitude, similar to findings of Abegaz *et al.* (2005) in Horro, Mohammadi *et al.* (2010) in Sanjabi, Mokhtari *et al.* (2013) in Arman, and Mahala *et al.* (2020) in Avikalin sheep.

All growth efficiency traits were statistically significant maternally correlated in present study, except ADG3-KR3 because maternal effects gradually declines as the animal grows.

CONCLUSIONS

The study revealed that the moderate heritability indicates that modest rates of genetic progress may be possible for average daily gain and Kleiber ratio from selection under the prevailing management system. The maternal influence diminished as age increases and maternal genetic effect (m^2) was found to be important and sizeable at weaning stage. This indicates that in order to crop more daily gain it is necessary to minimize the stress factors and protect animals from majority of variance inducing factors. To prevent the use of biased estimates of additive heritability especially when maternal effects are of high importance then total heritability (h^2_t), which takes direct heritability, maternal heritability and direct-maternal genetic correlation into account, could be used in estimation of breeding values and response to selection. Positive correlation between ADG and KR indicate the scope of indirect selection for ADG.

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