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Comparison of Reliability of Animal Models and Bayesian Approach for Estimation of Genetic Parameters of Growth Traits in Chokla Sheep

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

[1]Department of Animal Genetics and Breeding, College of Veterinary and Animal Science, RAJUVAS, Bikaner, Rajasthan, INDIA
[2]CSWRI- ARC, Beechwal, Bikaner, Rajasthan, INDIA
[3]ICAR-NDRI, Karnal, Haryana, INDIA
[4]Department of Livestock Production Management, College of Veterinary and Animal Science, RAJUVAS, Bikaner, Rajasthan, INDIA

**Corresponding author: G Choudhary; E-mail: drgarima2691@gmail.com*

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ABSTRACT

Data on 6785 Chokla sheep maintained at Central Sheep and Wool Research Institute, Bikaner, Rajasthan, India and recorded between 1974 and 2020, were collected for present study. Six different animal models used by wombat and BLUPF90 software (Bayesian method) were used to determine (co)variance components and genetic parameters of growth traits with various combinations of direct and maternal effects. Body weight at different age as birth (BW), 3(WW), 6 (6W), 9 (9W), 12 months of age (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) were used to study. The direct heritability estimates increased from birth to twelve months of age. Direct heritability estimates (from the best model as per AIC) for various growth traits ranged from 0.2 to 0.5 except for birth weight (0.17) by animal models. Highly inflated values of additive heritability were obtained in both methods due to negative and high estimate of correlation between additive and maternal effect. In this condition, it is more useful to use the total heritability (h^2_t) for evaluation of the response for selection based on phenotypic values to prevent the use of biased estimates of additive heritability. The maternal genetic effect (m^2) was found to be highest at birth weight by BLUPF90 and at weaning stage by animal model. Bayesian approach was found best as compared to WOMBAT for all traits to study (co)variance components and genetic parameters.

HIGHLIGHTS

- Compared reliability of animal models and bayesian approach for estimation of genetic parameters.
- Bayesian approach was found best as compared to WOMBAT for all traits to study (co)variance components and genetic parameters.

Keywords: Chokla, (Co) variance components, heritability, maternal genetic effect, WOMBAT, BLUPF90

Small ruminants serve the mankind in multiple ways of providing protein rich food, supplementing farmers' income, facilitating rural employment and improving soil fertility. So, these animals play an important role for the socio-economic upliftment of small, marginal farmers and landless labourers in our country. A number of non-genetic factors affect these growth traits and directly obscure recognition of the genetic potential. Improvement in production, without affecting adaptability can be brought about only by genetic improvement through selection and breeding. Formulation of breeding programmes require

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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).

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 (Gowane *et al.,* 2015; Aguirre *et al.,* 2016). 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. It was observed by various authors 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; Latifi and Mohammadi, 2018; Mahala *et al.,* 2020).

Carneiro *et al.* (2007) found that the Bayesian methodology is well justifiable for analysing small populations or data set when great 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; 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.

Hence, present study was undertaken to estimate various (co)variance components and genetic parameters for growth traits by animal models (wombat software) and Bayesian methodology (BLUPF90 software) as well as comparisons of reliability of both methods by various methods.

MATERIAL AND METHODS

Collections of data

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

Statistical analyses of data

Study of least squares-mean and effect of non genetic factors

The data were analysed to examine the effects of period (eleven period), season (spring and autumn), sex (male and female) 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:

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

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 $(0, \sigma^2)$

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

Estimation of (Co) variance components and corresponding genetic parameters

(Co)Variance components and corresponding genetic parameters for the studied traits were estimated by average information Restricted Maximum Likelihood (AIREML) using the WOMBAT programme (animal models) (Meyer, 2007) and BLUPF90 software (Bayesian methodology). In BLUPF90 software model 4 was not included in present study. 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
$Y = Xb + Z_1a + W_c + \varepsilon$		Model 4
$Y = Xb + Z_1a + Z_2m + Wc + \varepsilon$	with $Cov\,(a,m) = 0$	Model 5
$Y = Xb + Z_1a + Z_2m + Wc + \varepsilon$	with $Cov\,(a,m) = A\sigma_{am}$	Model 6

Where,

$Y = N \times 1$ vector of record

b = fixed effects in the model with association matrix X

a = vector of direct genetic effect with the association matrix Z_1

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

m = vector of maternal genetic effects with the association matrix Z_2

e = vector of residual (temporary environmental) effect

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

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

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

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

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

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

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

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

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

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

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

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

$$t_m = (1/4)\,h^2 + m^2 + c^2 + r_{am}\sqrt{m^2}\sqrt{h^2}\ ; \text{ (Al-Shorepy, 2001)}$$

Goodness of fit for the models

For wombat software results

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

Where log L_i is the maximised log likelihood of model i at convergence and p_i is the number of parameters obtained from each model; the model with the lowest AIC was chosen as the best approximating model.

For BLUPF90 software results

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).

Comparison of reliability of Animal model and Bayesian method

Best verses best model comparisons were studied which were found by WOMBAT and BLUPF90 software.

1. Comparison of CV (coefficient of variation in %) of different methods: The nearer the CV (%) of adjusted data to CV (%) of unadjusted data of trait, the more stable was the method.
2. By Coefficient of determination (R^2-value): method with highest coefficient of determination as compared to other methods was considered most accurate as compared to other methods.
3. The relative efficiency of each model as percent error variance of a model relative to the variance of most efficient model having least error variance.

Relative efficiency of each model (%) =

$$\frac{\text{Error variance of most efficient model} * 100}{\text{Error variance of other method}}$$

Method with lowest error variance was best and most efficient.

RESULTS AND DISCUSSION

One of the fundamental objectives of genetic evaluation exercises is to partition the genetic variance in direct and maternal effects, where applicable. The findings of the present study confirmed the importance of implementing the correct model for estimation of (co)variance components and genetic parameters for growth traits of Chokla sheep. Descriptive statistics of all traits was summarized in Table 1 and 2.

(Co) variance components and genetic parameter estimates by animal model

The findings of the present study confirmed the importance of implementing the correct model for estimation of (co) variance components and genetic parameters for growth traits of Chokla sheep. (Co)variance components and genetic parameters estimated by most appropriate model in univariate analysis by WOMBAT for various growth traits of Chokla sheep are summarized in Table 3.

The results presented in Table 3 show an incremental increase in (co)variance component and heritability values for the body weight traits according to the age of the animal. This trend was similar, but not of the same magnitude, as that reported by Mohammadi *et al.* (2015),

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

Trait	BW	WW	6W	9W	YW
No. of records	6769	5683	4911	4297	3689
Mean (kg)	2.88	13.64	19.32	21.30	24.36
Standard error	0.008	.051	.083	.092	.099
Minimum	1.25	7.00	10.00	12.00	14.00
Standard deviation	0.594	3.541	5.070	5.778	5.855
Maximum	5.00	28.80	40.00	45.00	46.60
CV%	20.62	25.96	26.24	27.12	24.03
Skewness	-0.20	-0.10	-0.13	0.22	0.06
Non genetic factors					
Period of lambing	**	**	**	**	**
Season of lambing	**	**	**	NS	**
Sex of lamb	**	**	**	**	**
Ewe's weight at lambing	**	**	**	**	**

** - Highly significant (P≤ 0.01); * - Significant (P≤0.05); NS- non significant.

Table 2: Descriptive statistics and data structure for ADG and KR in Chokla sheep

Trait		**ADG1/KR1 (0-3 months)**	**ADG2/KR2 (3-6 months)**	**ADG3/KR3 (6-12 months)**
No. of records		5674	4617	3094
Mean	ADG (gm/day)	118.70	64.95	30.61
	KR	16.43	6.80	2.71
Standard error	ADG	.550	.700	.490
	KR	.033	.056	.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
Non genetic factors				
Period of lambing		**	**	**
Season of lambing		**	**	**
Sex of lamb		**	**	**
Ewe's weight at lambing	ADG	**	NS	NS
	KR	**	**	**

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

Table 3: Estimated genetic parameters and (co)variance components from the best model for each trait

Traits	**Model**	**Genetic parameters**						**(co)variance components**					
		h^2	m^2	c^2	r_{am}	h_t^2	t_m	σ^2_a	σ^2_m	σ^2_c	σ^2_e	σ^2_p	σ_{am}
BW	6	0.173±0.031	0.168±0.031	0.121±0.019	-0.725±0.068	0.071	0.208	0.041	0.040	0.029	0.159	0.240	-0.029
WW	6	0.392±0.048	0.181±0.029	0.028±0.015	-0.915±0.033	0.118	0.063	2.905	1.343	0.209	4.76	7.418	-1.807
6W	3	0.471±0.045	0.130±0.023	—	-0.923±0.032	0.193	0.020	6.629	1.825	—	8.821	14.06	-3.211
9W	3	0.510±0.048	0.140±0.025	—	-0.914±0.032	0.213	0.023	6.791	1.863	—	7.907	13.310	-3.251
YW	3	0.515±0.052	0.170±0.029	—	-0.928±0.032	0.188	0.024	6.732	2.218	—	7.702	13.066	-3.587
ADG1	3	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	3	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	3	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	3	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	3	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	3	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

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

Gowane *et al.* (2015). Gowane *et al.* (2015) found that in Malpura sheep the h^2_a for weight at 90, 180, and 270 days was 0.40, 0.50, and 0.37, respectively and studies reported a negative direct-maternal correlation. 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. 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.

In most studies on growth traits, it has been frequently reported that direct heritability for body weights have a tendency to increase with age (Eskandarinasab *et al.*, 2010). The h^2 values for all the body weight traits except BW were moderate (0.3-0.5). The moderate heritability estimates for growth traits, ADG and Kleiber ratio of sheep in this study indicates that modest rates of genetic progress may be possible for these traits from selection under the prevailing management system.

The maternal genetic effect (m^2) was found to be important and sizeable at weaning stage. In these data, the maternal influence diminished as age increases, but modest genetic progress appears possible for all pre-weaning growth traits analyzed for the Chokla sheep. The maternal heritability estimated from model 6 for BW and WW and model 3 for remaining different body weight traits show a decreasing trend with advancement in age. The maternal effect is particularly important for early growth traits in sheep as it is influential during pregnancy and lactation, but its importance decreases during the post-weaning stages (Zishiri *et al.*, 2014; Gholizadeh and Ghafouri-Kesbi, 2015). When maternal effects are of high importance, total heritability values are more efficient than direct heritabilities for estimation of selection response based on phenotypic values.

The permanent environmental effect (c^2) of the dam on birth weight is mainly determined by uterine capacity, feeding level especially at late gestation. Maternal permanent environmental variance was found to influence the early body weight traits of BW and WW in present study.

(Co) variance components and genetic parameter estimates by Bayesian approach

As per DIC best model was found as model 3 for BW, 6W, ADG2, KR2 and KR3; model 5 for WW; model 6 for 9W, YW, ADG1, ADG3 and KR1.

Posterior mean, median and mode of various variance components and genetic parameters by best model for body weights, ADGs and KRs were summaried in Table 4, 5 and 6, respectively. Results showed that posterior mean, median and mode for all variance component and genetic parameters for all models were found approximate equal. So, it may be concluded that normal distribution was existed for all calculated (co)variance components and genetic parameters for all studied traits in present study.

An incremental increase in (co)variance component and heritability values for the body weight traits was found according to the age of the animal except for weaning weight (Table 4). At weaning weight, posterior mean of additive heritability was decreased as compared to birth weight due to maternal effect. 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).

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 4). 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 selecting animals. For ADG2 and ADG3, maternal effects had lesser role to play as compare to ADG1 for determining growth rate. Posterior mean of maternal effect (m^2) for corresponding KR 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. 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.

According to results of BLUPF90 software, maternal permanent environmental effect (c^2) was found to influence the weaning weight (0.023) and pre weaning average daily gain (0.017). 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 useful to use the total heritability (h^2_t) for evaluation of the response for selection based on phenotypic values to prevent the use of biased estimates of additive direct heritability.

Comparison of reliability of both methods

Coefficient of variation (%) of BW, WW and 6W was found more nearer to unadjusted CV in WOMBAT

Table 4: The posterior mean, median and mode of various variance components and genetic parameters for body weight at different age of Chokla sheep [standard deviations (PSD) of marginal posterior distribution of mean estimates are in brackets]

Trait	Items	Mean (PSD)	Median	Mode	HPD	MCE
BW	σ^2_a	0.044 (0.009)	0.044	0.050	0.027-0.062	0.0006
	σ^2_m	0.084 (0.008)	0.084	0.078	0.069-0.1006	0.0004
	σ_{am}	-0.041 (0.007)	-0.041	-0.042	-0.053 to (-0.025)	0.0005
	σ^2_c					
	σ^2_e	0.165 (0.006)	0.165	0.167	0.153-0.178	0.0004
	σ^2_p	0.294 (0.010)	0.294	0.295	0.274-0.315	0.0006
	h^2	0.151 (0.028)	0.151	0.156	0.098-0.208	0.0021
	m^2	0.286 (0.020)	0.286	0.270	0.251-0.323	0.0010
	c^2					
	h^2_t	0.083				
	t_m	0.182				
WW	σ^2_a	0.991 (0.187)	0.980	0.998	0.651-1.347	0.0139
	σ^2_m	0.289 (0.098)	0.288	0.290	0.107-0.491	0.0152
	σ_{am}	—	—	—	—	—
	σ^2_c	0.170 (0.096)	0.157	0.141	0.008-0.343	0.0183
	σ^2_e	5.907 (0.176)	5.906	5.963	5.581-6.269	0.0129
	σ^2_p	7.358 (0.150)	7.358	7.383	7.088-7.668	0.0085
	h^2	0.134 (0.024)	0.133	0.117	0.091-0.181	0.0017
	m^2	0.039 (0.013)	0.039	0.039	0.015-0.067	0.0020
	c^2	0.023 (0.013)	0.021	0.018	0.001-0.047	0.0025
	h^2_t	0.154	—	—	—	—
	t_m	0.095	—	—	—	—
6W	σ^2_a	6.687 (0.668)	6.706	6.893	5.388-8.005	0.0382
	σ^2_m	1.972 (0.293)	1.961	1.914	1.408-2.531	0.0266
	σ_{am}	-3.401 (0.409)	-3.402	-3.447	-4.338 to -2.7040	0.0359
	σ^2_c					
	σ^2_e	8.861 (0.397)	8.854	8.843	8.058-9.608	0.0280
	σ^2_p	17.520 (0.623)	17.509	17.392	16.439-18.864	0.0335
	h^2	0.381 (0.028)	0.3831	0.394	0.329-0.436	0.0019
	m^2	0.112 (0.014)	0.112	0.113	0.087-0.141	0.0014
	c^2					
	h^2_t	0.147	—	—	—	—
	t_m	0.014	—	—	—	—
9W	σ^2_a	6.819 (0.683)	6.799	6.308	5.509-8.113	0.0340
	σ^2_m	1.935 (0.352)	1.924	1.867	1.213-2.611	0.0359
	σ_{am}	-3.345 (0.450)	-3.333	-3.308	-4.280 to -2.498	0.0379
	σ^2_c	0.049 (0.065)	0.017	0.013	0.0006-0.1908	0.0168
	σ^2_e	7.869 (0.407)	7.87	7.87	7.004- 8.603	0.0203
	σ^2_p	16.672 (0.654)	16.61	16.532	15.567-18.008	0.0469
	h^2	0.408 (0.029)	0.408	0.409	0.353 -0.464	0.0016
	m^2	0.116 (0.018)	0.116	0.115	0.079-0.150	0.0019
	c2	0.003 (0.004)	0.001	0.0008	0.00003-0.011	0.0010
	h^2_t	0.166	—	—	—	—
	t_m	0.022	—	—	—	—

YW	σ^2_a	6.799 (0.688)	6.788	6.772	5.570-8.187	0.0332
	σ^2_m	2.148 (0.364)	2.117	1.913	1.475-2.869	0.0421
	σ_{am}	-3.650 (0.428)	-3.660	-3.524	-4.435 to -2.782	0.0287
	σ^2_c	0.239 (0.178)	0.198	0.093	0.010-0.590	0.0481
	σ^2_e	7.552 (0.415)	7.559	7.660	6.762- 8.356	0.0333
	σ^2_p	16.738 (0.663)	16.746	16.704	15.446-18.006	0.0435
	h^2	0.405 (0.029)	0.405	0.386	0.355-0.468	0.0016
	m^2	0.128 (0.018)	0.127	0.118	0.098-0.170	0.0023
	c^2	0.014 (0.011)	0.012	0.002	0.0006-0.0355	0.0029
	h^2_t	0.143	—	—	—	—
	t_m	0.026	—	—	—	—

σ^2_a, σ^2_m, σ^2_c, σ^2_e and σ^2_p are additive genetic, maternal additive genetic, maternal permanent environmental, residual variance and phenotypic variance, respectively; h^2 is heritability; c^2 is σ^2_c/σ^2_p; m^2 maternal heritability is σ^2_m/σ^2_p; σ_{am} – direct-maternal genetic covariance; t_m is maternal across year repeatability for ewe performance; h^2_t is total heritability; PSD- posterior standard deviation; HPD- high probability density; MCE- monte carlo error

Table 5: The posterior mean, median and mode of various variance components and genetic parameters for average daily gain of Chokla sheep [standard deviations (PSD) of marginal posterior distribution of mean estimates are in brackets]

Trait	Items	Mean (PSD)	Median	Mode	HPD	MCE
ADG1	σ^2_a	328.99(48.037)	329.10	335.23	234.20-423.70	2.7934
	σ^2_m	138.92(24.979)	139.90	145.01	88.920-182.00	2.9179
	σ_{am}	-191.11(30.464)	-191.00	-186.19	-249.30 to -132.10	2.1352
	σ^2_c	17.327(10.068)	16.920	20.913	2.056-36.230	1.7522
	σ^2_e	556.56(27.915)	557.40	559.00	500.00-607.20	1.4817
	σ^2p	1041.8(43.167)	1042.8	1047.0	959.77-1130.4	2.7009
	h^2	0.315(0.035)	0.316	0.322	0.248- 0.387	0.0020
	m^2	0.133(0.020)	0.134	0.143	0.092-0.169	0.0026
	c^2	0.017(0.010)	0.016	0.019	0.002-0.035	0.0017
	h^2_{t}	0.107	—	—	—	—
	t_m	0.046	—	—	—	—
ADG2	σ^2_a	413.26(46.216)	411.90	409.73	316.90-501.50	2.3222
	σ^2_m	109.42(13.014)	109.10	108.44	83.640-134.70	0.9493
	σ_{am}	-212.31 (24.136)	-211.40	-223.75	-259.60 to -162.50	1.2680
	σ^2_c					
	σ^2_e	574.62(26.994)	574.40	568.29	525.80- 631.60	1.3605
	σ^2p	1097.3(41.059)	1098.6	1097.9	1019.9-1178.4	2.0501
	h^2	0.376(0.030)	0.376	0.366	0.320-0.439	0.0015
	m^2	0.099(0.009)	0.099	0.099	0.083- 0.119	0.0007
	c^2					
	h^2_{t}	0.136	—	—	—	—
	t_m	0.001	—	—	—	—

ADG3	σ^2_a	73.189(10.519)	72.850	70.860	53.410-92.130	0.5724
	σ^2_m	30.268(4.875)	30.220	30.471	20.710-39.460	0.5457
	σ_{am}	-46.791 (7.079)	-46.440	-45.543	-60.280 to -33.700	0.6585
	σ^2_c	1.344(1.189)	0.963	0.247	0.035-3.810	0.1737
	σ^2_e	130.01(6.929)	129.80	126.70	115.90-142.20	0.4301
	$\sigma^2 p$	234.82(10.992)	234.60	244.26	213.79-255.42	0.6240
	h^2	0.310(0.032)	0.310	0.296	0.247-0.365	0.0018
	m^2	0.128(0.016)	0.129	0.131	0.098-0.159	0.0019
	c^2	0.006(0.005)	0.004	0.001	0.0001-0.0160	0.0007
	h^2_t	0.077	—	—	—	—
	t_m	0.014	—	—	—	—

Footnote same as Table 4.

Table 6: The posterior mean, median and mode of various variance components and genetic parameters for kleiber ratio of Chokla sheep [standard deviations (PSD) of marginal posterior distribution of mean estimates are in brackets]

Trait	Items	Mean(PSD)	Median	Mode	HPD	MCE
KR1	σ^2_a	1.242(0.187)	1.241	1.244	0.884-1.610	0.0111
	σ^2_m	0.426(0.084)	0.431	0.411	0.269-0.598	0.0100
	σ_{am}	-0.588(0.109)	-0.584	-0.542	-0.797 to -0.361	0.0077
	σ^2_c	0.038(0.030)	0.032	0.007	0.001-0.099	0.0059
	σ^2_e	2.030(0.107)	2.030	2.066	1.832-2.248	0.0061
	$\sigma^2 p$	3.735(0.155)	3.739	3.746	3.484-4.094	0.0098
	h^2	0.331(0.039)	0.332	0.330	0.258 -0.408	0.0022
	m^2	0.113(0.019	0.115	0.111	0.076-0.152	0.0025
	c^2	0.010(0.008)	0.008	0.001	0.0003-0.0262	0.0016
	h^2_t	0.153	—	—	—	—
	t_m	0.050	—	—	—	—
KR2	σ^2_a	2.654(0.306)	2.655	2.668	1.993- 3.167	0.0144
	σ^2_m	0.794(0.123)	0.792	0.783	0.549- 1.022	0.0253
	σ_{am}	-1.442 (0.188)	-1.436	-1.447	-1.823-(-1.111)	0.0268
	σ^2_c					
	σ^2_e	3.684(0.187)	3.676	3.667	3.279-4.003	0.0088
	$\sigma^2 p$	7.132(0.283)	7.124	7.108	6.553 -7.674	0.0162
	h^2	0.371(0.031)	0.372	0.389	0.305-0.425	0.0014
	m^2	0.111(0.014)	0.111	0.109	0.085-0.140	0.0031
	c^2					
	h^2_t	0.124	—	—	—	—
	t_m	.002	—	—	—	—

KR3	σ^2_a	0.448(0.067)	0.449	0.418	0.319-0.566	0.0031
	σ^2_m	0.170(0.036)	0.168	0.166	0.105- 0.242	0.0042
	σ_{am}	-0.267(0.044)	-0.269	-0.270	-0.351-(-0.182)	0.0030
	σ^2_c					
	σ^2_e	0.758(0.041)	0.756	0.750	0.682-0.839	0.0019
	$\sigma^2 p$	1.376(0.067)	1.372	1.339	1.263-1.522	0.0037
	h^2	0.324(0.037)	0.326	0.310	0.244-0.385	0.0022
	m^2	0.123(0.021)	0.123	0.114	0.084-0.164	0.0028
	c^2					
	h^2_t	0.096	—	—	—	—
	t_m	0.011	—	—	—	—

Footnote same as Table 4.

Table 7: Comparison of reliability of the most appropriate models by WOMBAT and BLUPF90 softwares

Trait	Best model	Comparison of CV (%)		Coefficient of determination (R2 in %)	Error variance	Relative efficiency
		Unadjusted data	Adjusted data			
BW						
WOMBAT	6	20.62	13.80	0.333	**0.159**	**1**
BLUPF90	3	20.62	**14.05**	**0.438**	0.165	0.963
WW						
WOMBAT	6	25.96	16.01	**0.357**	**4.768**	**1**
BLUPF90	5	25.96	**17.81**	0.197	5.907	0.807
6W						
WOMBAT	3	26.24	15.37	0.372	**8.821**	**1**
BLUPF90	3	26.24	**15.41**	**0.494**	8.861	0.995
9W						
WOMBAT	3	27.12	**13.20**	0.405	7.907	0.995
BLUPF90	6	27.12	13.17	**0.528**	**7.869**	**1**
YW						
WOMBAT	3	24.03	11.40	0.410	7.702	0.980
BLUPF90	6	24.03	11.28	**0.549**	**7.552**	**1**
ADG1						
WOMBAT	3	30.91	**20.06**	0.329	567.52	0.980
BLUPF90	6	30.91	19.87	**0.466**	**556.56**	**1**
ADG2						
WOMBAT	3	51.69	**37.08**	0.342	580.17	0.990
BLUPF90	3	51.69	36.90	**0.476**	574.62	1
ADG3						
WOMBAT	3	50.60	**37.57**	0.294	132.26	0.982
BLUPF90	6	50.60	37.24	**0.446**	**130.01**	**1**
KR1						
WOMBAT	3	12.65	**8.73**	0.344	2.058	0.986

Trait	Best model	Comparison of CV (%)		Coefficient of determination (R2 in %)	Error variance	Relative efficiency
		Unadjusted data	Adjusted data			
BLUPF90	6	12.65	8.67	**0.454**	**2.030**	**1**
KR2						
WOMBAT	3	37.66	28.36	0.346	3.720	0.990
BLUPF90	3	37.66	28.22	**0.483**	**3.684**	**1**
KR3						
WOMBAT	3	40.99	**32.29**	0.304	0.766	0.989
BLUPF90	3	40.99	32.12	**0.449**	**0.758**	**1**

method as compared to Bayesian (BLUPF90) method. So for study of these traits WOMBAT is more reliable than Bayesian approach. While, for remaining traits CV of adjusted data were found nearer to CV of unadjusted data in BLUPF90 as compared to WOMBAT. So for study of these remaining traits Bayesian method was found more reliable than WOMBAT.

According to values of R2 BLUPF90 was found best as compared to WOMBAT for all the traits to study (co) variance components and genetic parameters except weaning weight, for which WOMBAT was found better.

Relative efficiency of models used by WOMBAT was higher than Bayesian methods for BW, WW and 6W. For remaining traits relative efficiency of models used by Bayesian approach was higher than WOMBAT.

CONCLUSION

The study revealed that the moderate heritability indicates that modest rates of genetic progress may be possible for these traits from selection under the prevailing management system. The maternal influence diminished as age increases and maternal genetic effect was found to be important and sizeable at weaning stage. It is more useful to use the total heritability for evaluation of the response for selection based on phenotypic values to prevent the use of biased estimates of additive heritability caused by high and negative correlation between additive and maternal effect. After comparison of reliability of bayesian and WOMBAT, bayesian approach was found more reliable method for mostly traits than WOMBAT.

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