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Estimates of (Co) variance components and genetic parameters for growth traits of Malpura sheep in semi-arid region of Rajasthan

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Abstract

The aim of present study was to estimate (Co) variance components and genetic parameters of weight at birth (BWT), weaning (3WT), 6, 9 and 12 months of age (6WT, 9WT and 12WT, respectively) of Malpura sheep, maintained at Central Sheep and Wool Research Institute, Avikanagar, Rajasthan, India, by restricted maximum likelihood. Six different animal models with various combinations of direct and maternal effects were used. Data were collected over a period of 45 years (1975 to 2019). A log-likelihood ratio test was used to select the most appropriate univariate model for each trait, which was subsequently used in bivariate analysis. Heritability estimates for BWT, 3WT, 6WT, 9WT and 12WT were 0.15±0.02, 0.13±0.02, 0.18±0.02, 0.18±0.02 and 0.16±0.03, respectively. Maternal permanent environmental effect contributed 13% for BWT and 7% for weaning weight. There was no evidence for maternal permanent environmental effect on the post-weaning body weights. A moderate rate of genetic progress seems possible in the flock through selection. Direct genetic correlations between body weight traits were positive and ranged from 0.12 between BWT and 9WT to 0.80 between 3WT and 6WT. The high positive genotypic and phenotypic correlations between body weight at six months, nine months and twelve months of age indicates that selection for six months of traits will result in increase in nine and twelve months of body weight.

Keywords: Heritability, correlation, genetic, phenotypic, maternal effects, malpura sheep

1. Introduction

Rajasthan with 7.9 million of sheep population (Livestock Census 2020) is the 4th largest sheep rearing state (10.63% of total sheep of India) of the country. Sheep production is the major occupation of rural people especially in the semi-arid region of India. Malpura sheep are one of the heaviest sheep breed in India, known for their adaptability to the harsh environment and potential for high meat production (Mishra, 2008) [14]. They are mainly reared for mutton production, as the earnings from the wool are of little market value mainly due to unavailability of good market followed by coarse texture of wool. Malpura sheep are widely distributed in the semi-arid region of Rajasthan, mostly in the Tonk, Jaipur and Sawai Madhopur districts. Malpura sheep are reared by small and marginal land holders who graze them on fallow land, crop residue and also take them on migration during periods when grazing resources are scarce. According to Breed survey 2022, the total population of Malpura sheep was estimated as 209534 number including 85443 pure and 124091 graded animals. The growth potential of the lambs is very important in the sheep production. It is essential to have knowledge of genetic parameters for these economically important traits to formulate optimum breeding strategies for better production. Growth traits are influenced both by direct additive genetic effects and by maternal effects (Albuquerque and Meyer, 2001) [2]. Traits recorded in early life are likely to be affected by maternal ability (Robison, 1981) [21]. Nasholm and Danell (1994) [17] observed that when maternal genetic effects are important and not considered in the statistical model, heritability estimates are biased upward and the realized efficiency of selection is reduced when compared with the expected. Thus for achieving optimum progress especially in growth traits, both direct and maternal components must be considered. Keeping in view of the above economic consequences of Malpura sheep, the present investigation was planned to estimate the genetic and phenotypic parameters for growth traits of Malpura sheep.

2. Materials and Methods

2.1. Description of data, location and farm management

Data were collected from the available database (Pedigree and growth performance) of Malpura sheep presently maintained under Mega Sheep Seed Project (MSSP) at the Animal Genetics and Breeding Division of ICAR-Central Sheep and Wool Research Institute (CSWRI), Avikanagar. The farm is situated in the block Malpura, District Tonk of Rajasthan, India at 75°28' E Latitude and 26°17' N Longitude and at an altitude of 320 m above mean sea level. The climate is semi-arid and subtropical in nature with the extreme temperature variation of maximum 45 °C to a minimum temperature of 4 °C across year. The annual rainfall was 615.93 mm.

A total record of 8299 lambs of Malpura sheep born from 2529 dams and 525 sires spread over a period of 45 years (1975–2019) comprised the material for this study. The animals were kept under semi-intensive management system. The flock was a closed type where around 300 breeding females were maintained over the years. Male to female ratio for breeding was around 1:25. The castration of ram lambs was not practiced at the farm. Animals were shorn twice in a year in March and September.

The lambing seasons were major in spring early January to mid March and minor in autumn (August–September). At lambing, records of both lambs and dams' weight, lambing date, sex and type of birth of each lamb were taken. After lambing, lambs were kept with their dams for around one week. From three weeks of age until weaning, lambs were kept separate and allowed to be nursed two times per day, and lambs were grazed separately from their dams for 3 h each in morning and evening. Weaning of lambs from their dams were performed at an average three month of age. After weaning the male and female lambs were segregated and housed separately. In addition to 8–10 h of grazing and dry fodder supplementation, concentrate mixture was also supplemented based upon their age, sex, and production stage. The lambs were regularly drenched and dipped to control internal and external parasites, respectively. The animals were routinely vaccinated against *peste des petits ruminants* (PPR), enterotoxaemia (ET) and foot-and-mouth disease (FMD).

For the final analysis, the growth data were categorized into 9 periods of 5 years interval each as [P1 (1975 to 1979), P2 (1980 to 1984), P3 (1985 to 1989), P4 (1990 to 1994), P5 (1995 to 1999), P6 (2000 to 2004), P7 (2005 to 2009), P8 (2010 to 2014) and P9 (2015 to 2019)]. The data recorded were classified in 4 parity groups. The observations of parity of 4 and above were merged in the parity 4 due to less number of observations in higher parities. The data recorded were divided in 2 seasons of lambing as Major spring (January–March) and minor autumn (August–September) season. The five different economic growth traits used for the genetic analysis were birth weight (BWT), weaning weight (WWT), 6 months weight (6WT), 9 months weight (9WT) and 12 months weight (12WT). The Characteristics of the pedigree and data structure, least squares mean (LSM), standard deviation and coefficient of variance (CV %) for weights at different ages are illustrated in Table 1.

2.2. Statistical analysis of data

The influence of various non-genetic factors, i.e. period of birth, sex of lambs, season of lambing and parity of dam on different growth performance traits and to overcome the problem of non orthogonality of effects due to unequal and disproportionate sub-class frequencies, least square technique (SPSS 25.0) was employed. Dam's weight at lambing was used as linear covariate. All the fixed effects were found to be significant in the analysis, hence all the effects were included in the linear mixed models which were subsequently used for the genetic analysis. Variance and (co) variance components for additive direct and maternal direct effect were estimated by restricted maximum likelihood procedures (REML) using derivative free algorithm fitting an animal model for growth traits. The analysis was worked out by the WOMBAT approach (Meyer 2007). Univariate animal models were fitted to estimate (co) variance components for all the traits. Convergence of the REML solutions was assumed when the variance of function values (–2 logL) in the Simplex was less than 10^{-8}. To ensure that a global maximum was reached, analyses were restarted. When estimates did not change, convergence was confirmed. Six models which accounted for the direct and maternal effects were fitted as follows:

Different models which account for the direct and maternal effects were constructed as below

1. $y = X\beta + Z_a a + \varepsilon$
2. $y = X\beta + Z_a a + Z_m m + \varepsilon$ with $Cov(a_m, m_o) = 0$
3. $y = X\beta + Z_a a + Z_m m + \varepsilon$ with $Cov(a_m, m_o) = A\sigma_{am}$
4. $y = X\beta + Z_a a + Z_{pe} pe + \varepsilon$
5. $y = X\beta + Z_a a + Z_m m + Z_{pe} pe + \varepsilon$ with $Cov(a_m, m_o) = 0$
6. $y = X\beta + Z_a a + Z_m m + Z_{pe} pe + \varepsilon$ with $Cov(a_m, m_o) = A\sigma_{am}$

Where y is the vector of records; β, a, m, pe and ε are vectors of fixed, direct additive animal genetic, maternal additive genetic, permanent environmental effects of the dam, and residual effects, respectively; with association matrices X, Z_a, Z_m and Zpe; A is the numerator relationship matrix between animals; and $\sigma_{am}$is the covariance between additive direct and maternal genetic effects. Assumptions for variance (V) and covariance (Cov) matrices involving random effects were

$V(a) = A\sigma^2_a$, $V(m) = A\sigma^2_m$, $V(c) = I\sigma^2_c$, $V(e) = I\sigma^2_e$, and $Cov(a,m) = A\sigma_{am}$

Where I is an identity matrix and σ^2_a, σ^2_m, σ^2_c and σ^2_e are additive direct, additive maternal, maternal permanent environmental and residual variances, respectively. The best model suited for each trait considering the Likelihood Ratio Test (LRT) was chosen for estimation of genetic parameters (Meyer, 1997) [13]. Maternal across year repeatability for ewe performance ($t_m = 0.25\ h^2 + m^2 + c^2 + m\ r_{am}h$) was calculated. The total heritability (h_t^2) was also be calculated using the formula $h_t^2 = (\sigma^2_a + 0.5\sigma^2_m + 1.5\ \sigma_{am}) / \sigma^2_p$; (Willham, 1972) [24]. An effect was considered to have a significant influence when its inclusion caused a significant increase in log likelihood, compared with the model in which it was ignored. Significance was tested at $P<0.05$, by comparing differences in log likelihoods to values for a chi-squared distribution with degrees of freedom equal to the difference in the number of (co) variance components fitted for the two models. The most appropriate model for each trait as per LRT, (Meyer, 1997) [13] was subsequently used in the bivariate analyses for the estimation of genetic and phenotypic correlations between the traits with starting values derived from single trait analyses.

Table 1: Characteristics of data structure for growth traits of Malpura sheep

Items	BWT	WWT	6WT	9WT	12WT
No. of records	8299	7251	6371	5324	4709
Sires with progeny records	525	517	503	490	485
Dams with progeny records	2529	2399	2276	2105	1989
Mean (kg)	3.06	14.50	21.92	25.02	28.11
Standard deviation	0.62	3.95	5.55	5.79	6.14
Coefficient of variation (CV %)	20.47	26.87	24.72	22.62	21.16

BWT = birth weight; WWT = weaning weight; 6WT = 6 months weight; 9WT= 9 months weight; 12WT = 12 months weight.

3. Results and Discussion
Least squares means along with the standard deviation (s.d.) and percent coefficient of variation for different traits under study are given in Table 1. The least squares mean for various traits were BWT 3.06 kg; 3WT 14.50 kg; 6WT 21.92 kg; 9WT 25.02 kg and 12WT 28.11 kg.

(Co) variance components and genetic parameters estimated by best model in univariate analysis for various traits of Malpura sheep are presented in Table 2. As per LRT, the best model for BWT, 3WT, 6WT, 9WT and 12WT was Model-5, where phenotypic variance is partitioned in to direct additive, direct maternal and maternal permanent environmental effect.

Table 2: Estimates of (Co) variance components (kg^2) and genetic parameters for body weight traits of Malpura sheep using best univariate model

Item	BWT	3WT	6WT	9WT	12WT
Additive variance (σ^2_a)	0.04±0.01	1.43±0.23	3.50±0.45	3.64±0.49	3.43±0.52
Maternal variance (σ^2_m)	0.04±0.01	0.38±0.15	1.05±0.30	1.57±0.40	1.29±0.38
σ^2_c	0.03±0.01	0.77±0.16	0.00±0.28	0.00±0.36	0.00±0.39
σ^2_e	0.16±0.01	7.81±0.21	14.43±0.42	15.04±0.48	15.86±0.53
σ^2_p	0.29±0.01	10.40±0.2	18.99±0.37	20.26±0.43	20.59±0.46
h^2	0.15±0.02	0.13±0.02	0.18±0.02	0.18±0.02	0.16±0.03
m^2	0.11±0.02	0.03±0.02	0.05±0.02	0.07±0.02	0.06±0.02
c^2	0.13±0.02	0.07±0.02	0.00	0.00	0.00
h^2_t	0.23	0.16	0.21	0.22	0.20
t_m	0.29	0.14	0.10	0.123	0.10
LogL	1543.993	-11960.980	-12405.253	-10528.223	-9380.427

σ^2_a, σ^2_m, σ^2_c, σ^2_e and σ^2_p are additive direct, maternal genetic, maternal permanent environmental, residual variance and phenotypic variance, respectively; h^2 is heritability; m^2 is $\sigma^2 m$ / $\sigma^2 p$; c^2 is $\sigma^2 c$/ $\sigma^2 p$; t_m is maternal across year repeatability for ewe performance; r_{am} is direct–maternal correlation; h^2T is total heritability and logL is log likelihood.

3.1. Birth weight
Additive genetic variance for the BWT was low. In the Model 5, h^2 for BWT was 0.15±0.02. The low heritability estimate for BWT may be attributed to the general poor nutritional level of ewes giving a leeway for large environmental variation. The current h^2 estimate for BWT was lower than the earlier reported estimate (0.29) by Mishra *et al*. (2009) [15] for Malpura sheep by paternal half sib method. The estimate by Mishra *et al*. (2009) [15] was likely inflated due to ignorance of the maternal effects in the model. The heritability estimate for BWT was similar to average weighted estimates reviewed by Safari *et al*. (2005) [22] for various wool breeds (0.21), dual-purpose breeds (0.19) and meat breeds (0.15).

Estimate of maternal permanent environmental effect (c^2) was (0.13±0.02). The estimate for c^2 was similar to the average values reviewed by Safari *et al*. (2005) [22] for various sheep breeds, estimate by Mandal *et al*. (2006) [9] for Muzaffarnagri sheep and Gowane *et al*. (2010a) [4] for Bharat Merino sheep. Estimates of h^2_t was 0.23 for BWT in Malpura sheep which was within the range of estimates by Bromley *et al*. (2000), Neser *et al*. (2001), Safari *et al*. (2005) [22] for various sheep breeds and Kushwaha *et al*. (2009) [8] for Chokla sheep. The estimate of repeatability of ewe performance (t_m) for BWT was 0.29 for the Malpura sheep. Our maternal repeatability estimate for BWT was comparable with the values reported by Mandal *et al*. (2006) [9], Kushwaha *et al*. (2009) [8] and Gowane *et al*. (2010a) [4].

The moderate estimate of direct heritability suggests that birth weight of Malpura sheep can be improved through selection. The modest c^2 estimate indicates the importance of maternal environment and maternal care at birth of the lamb. Actual partitioning of the maternal variance in additive and permanent environmental effects was practically difficult. Maternal effects were important at birth, most likely reflecting differences in the uterine environment and the quality and capacity of the uterine space for growth of the fetus. In the Malpura sheep, partitioning of the overall ewe effect into its components was much more challenging, probably requiring more repeated records on related ewes. Particularly for m^2 and c^2, there was almost certainly a negative covariance between the estimates. This occurred because the estimates were not independent, and because a very good data structure is required to estimate both accurately. Estimate of repeatability of ewe performance were normally much more stable than the component estimates of m^2 and c^2. Moderate estimates of h^2_t and t_m suggest scope of improvement in the BWT through mass selection in Malpura sheep.

3.2. Weaning weight
Genetic parameters and (co) variance components for weaning weight along with log-likelihood values are presented in Table 2. In the more comprehensive model 5, estimates of h^2, m^2 and c^2 were 0.13, 0.03 and 0.07, respectively. The direct heritability estimate for WWT was similar to the earlier estimate reported by Mishra *et al*. (2009) [15] for Malpura sheep by paternal half sib analysis. Estimates were higher as reported by Mandal *et al*. (2006) [9] in

Muzaffarnagri sheep (0.21) and Kushwaha *et al*. (2009) [8] in Chokla sheep (0.18). Lower estimates than current study were obtained by Maroof *et al*. (2005) [12] for Avikalin sheep (0.08) and Gowane *et al*. (2010a) [4] for Bharat Merino sheep (0.04±0.02). The estimate of 0.07±0.02 for c^2 in the current study was in congruence with the reports by Safari *et al*. (2005) [22] for various wool and dual-purpose sheep breeds (0.06, 0.07), Kushwaha *et al*. (2009) [8] reported similar c^2 estimate (0.03-0.07) in Chokla sheep and Gowane *et al*. (2010a) [4] in Bharat Merino sheep (0.06±0.02). A decline in the importance of maternal effects from birth to weaning was reported earlier by Safari *et al*. (2005) [22], Mandal *et al*. (2006) [9] and Kushwaha *et al*. (2009) [8]. Estimate of t_m was low in present study (0.14) for Malpura sheep. In the current study estimate of h^2_t was moderate (0.16), which was in congruence with the reports of Notter (1998) [19] for Suffolk sheep (0.19) and Kushwaha *et al*. (2009) [8] for Chokla sheep (0.18). Moderate additive variability for WWT in Malpura sheep and also the estimate of tm and h^2_t indicates further scope of genetic improvement in weaning weight through mass selection.

3.3. Post-weaning weights
Estimates of (co) variance components were calculated for the weights at 6, 9 and 12 months of age (Table 2). The direct heritability estimate from the best model (model 5) for post-weaning weights were 0.18±0.02 at 6WT, 0.18±0.02 at 9WT and 0.16±0.03 at 12WT for Malpura sheep. Gowane *et al*. (2010b) [5] reported a slightly higher estimate of h^2 at 6WT for Malpura sheep (0.27). The current estimate of h^2 agrees well with the findings of Safari *et al*. (2005) [22] for various wool, meat and dual-purpose breeds (0.30, 0.28 and 0.22, respectively); and Maroof *et al*. (2005) [12] for Avikalin sheep (0.16 and 0.20 for 6WT and 12WT, respectively). There was no evidence for the maternal permanent effect on post-weaning weights at any age. This is indicative of the fact that the post weaning period has almost no carryover maternal effect and indicates the importance of the impact of the animal's own genotype for body weight at the post weaning stage. Similar reports where maternal effects were found to be declining with the advancement of age were given by Maria *et al*. (1993) [11], Tosh and Kemp (1994) [23], Mortimer and Atkins (1994) [16], Mandal *et al*. (2006) [9] and Mandal *et al*. (2009) [10].

Table 3: Estimated Genetic correlations (above diagonal) and phenotypic correlation (below diagonal) among body weight from bivariate analysis

Trait	BWT	WWT	6WT	9WT	12WT
BWT	1	0.27±0.09	0.18±0.09	0.12±0.09	0.21±0.09
WWT	0.39±0.01	1	0.80±0.03	0.63±0.06	0.54±0.07
6WT	0.28±0.01	0.76±0.00	1	0.84±0.02	0.68±0.05
9WT	0.24±0.01	0.62±0.00	0.83±0.00	1	0.87±0.02
12WT	0.24±0.01	0.53±0.01	0.70±0.01	0.84±0.00	1

Our estimates of repeatability of ewe performance (t_m) for Malpura sheep were low (0.10, 0.12 and 0.10) for 6WT, 9WT and 12WT. Gowane *et al*. (2010b) [5] reported similar estimates for these traits. Total heritability (h^2_t) estimates for Malpura sheep were 0.21, 0.22 and 0.20 for 6WT, 9WT and 12WT, respectively in the current study. Our estimates are within the range of earlier reports by Ozcan *et al*. (2005) [20], Safari *et al*. (2005) [22] and Gowane *et al*. (2010b) [5]. Results suggest scope of further genetic improvement in post-weaning weights by selection.

3.4. Correlation estimates
Direct genetic correlations between body weight traits were positive and ranged from 0.12 between BWT and 9WT to 0.80 between 3WT and 6WT (Table 3). The estimates of genetic correlations of BWT with body weight up to 12 months were low to moderate. The genetic correlation of WWT with post-weaning weights were high to moderate (WWT–6WT=0.80, WWT–9WT=0.63, and WWT–12WT=0.54). The genetic correlations between other weight traits (6WT to 12WT) were also high (positive) ranging from 0.84 for 6WT–9WT to 0.87 for 9WT–12WT. The genetic correlation estimate of 0.27 for BWT–WWT was lower with the estimate of 0.52 by Hanford *et al*. (2003) in Targhee sheep and 0.45 by Gowane *et al*. (2010a) [4] in Bharat Merino sheep. The estimates for phenotypic correlation between different body weight traits were positive and medium to large. High genetic correlation between body weight traits suggests that many of the genetic factors that influence body weight at weaning to adult stage were the same. On the basis of the high genetic correlation of 6WT with 9WT and 12WT, it can be said that animals with above average 6WT would tend to be above average in genetic merit for 9WT and 12WT. Selecting animals at weaning has a drawback of persisting maternal effect at that stage.

Therefore in spite of having positive genetic association of WWT with other traits, such selection criteria cannot be suggested. Thus it is recommended to practice a single trait selection using only 6WT in Malpura sheep looking into the results obtained and the mutton type characteristics of the sheep.

4. Conclusion
The moderate to high estimates of heritability and genetic correlation for live weight traits at different ages is suggestive of genetic improvement in these traits by selection at an appropriate age. Maternal genetic effects seemed to be significant across the traits; however, permanent environment had its role to play only at birth and the effect faded thereafter. The maternal permanent environment effect although was low for WWT, but it will still influence the expression of individual's real phenotype due to masking effects of pre-weaning care and kin/contemporary competition. Therefore 6WT seems to be the best age of criteria for selection in the Malpura sheep looking into the importance of this breed as a major mutton type sheep breed of semi-arid region of India.

5. Conflict of interest
The authors declare that there are no conflicts of interest.

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