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REGULAR ARTICLES

Estimates of direct and maternal (co)variance components as well as genetic parameters of growth traits in Nellore sheep

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Abstract In the present study, (co)variance components and genetic parameters in Nellore sheep were obtained by restricted maximum likelihood (REML) method using six different animal models with various combinations of direct and maternal genetic effects for birth weight (BW), weaning weight (WW), 6-month weight (6MW), 9-month weight (9MW) and 12-month weight (YW). Evaluated records of 2075 lambs descended from 69 sires and 478 dams over a period of 8 years (2007–2014) were collected from the Livestock Research Station, Palamaner, India. Lambing year, sex of lamb, season of lambing and parity of dam were the fixed effects in the model, and ewe weight was used as a covariate. Best model for each trait was determined by log-likelihood ratio test. Direct heritability for BW, WW, 6MW, 9MW and YW were 0.08, 0.03, 0.12, 0.16 and 0.10, respectively, and their corresponding maternal heritabilities were 0.07, 0.10, 0.09, 0.08 and 0.11. The proportions of maternal permanent environment variance to phenotypic variance (Pe^2) were 0.07, 0.10, 0.07, 0.06 and 0.10 for BW, WW, 6MW, 9MW and YW, respectively. The estimates of direct genetic correlations among the growth traits were positive and ranged from 0.44(BW-WW) to 0.96(YW-9MW), and the estimates of phenotypic and environmental correlations were found to be lower than those of genetic correlations. Exclusion of maternal effects in the model resulted in biased estimates of genetic parameters in Nellore sheep. Hence, to implement optimum breeding strategies for improvement of traits in Nellore sheep, maternal effects should be considered.

Keywords (Co)variance components · Genetic correlations · Maternal effects · Nellore sheep · REML

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Introduction

Sheep contributes significantly to the livelihood of small and marginal farmers and landless laborers in rural areas of arid and semi-arid regions of India. Nellore sheep are tallest among 42 recognized breeds in India and distributed in Prakasham, Guntur and Nellore districts of Andhra Pradesh state with a population of 11.74 million that accounts to 19.17% of total sheep population in the country. Nellore sheep can perform better under poor quality range conditions, adapted to local conditions and possess good disease resistance.

Nellore sheep meat is the preferred choice of consumers; hence, their growth performance is important for earning better profits by the owners. Growth potential of an animal is determined by its own genes and also by the dam's genes (Albuquerque and Meyer 2001). Dam's milk production and mothering ability are the maternal components affecting the birth weight and pre-weaning growth of lambs. Ignoring maternal effects in genetic evaluation of tropical sheep breeds (Robison 1981; Nasholm and Danell 1994; Wasike et al. 2009) results in inflated estimates of genetic parameters and, in turn, leads to reduced selection efficiency (Dodenhoff et al. 1999; Maniatis and Pollott 2002).

Few research works reported direct and maternal effects for different growth traits in several Indian sheep breeds, viz. Muzaffarnagri, Chokla, Malpura, Avikalin, Bharat Merino and Marwari sheep (Mandal et al. 2006a, b; Kushwaha et al. 2009; Gowane et al. 2010a; Prince et al. 2010; Gowane et al. 2010b; Singh et al. 2016). Although, the Nellore sheep population was maintained over the years through selection, seldom explored the underlying factors influencing the growth traits involving the maternal component in this breed. Hence, the objectives of the study were to identify the various environmental factors influencing the growth performance and to estimate variance and covariance components pertaining to direct and maternal effects for various body weights with combination of different effects in this sheep. Genetic, phenotypic and environmental correlations between traits were also estimated.

Materials and methods

Data collection

Data for a period of 8 years (year 2007 to 2014) were collected from the flock of Nellore sheep maintained at the Livestock Research Station, Palamaner, Andhra Pradesh, India (13°.20′ E latitude and 78°.75′N longitude and altitude 683 m MSL). Growth traits used for the analysis were birth weight (BW), weaning (WW), 6 months (6MW), 9 months (9MW) and 12 months (YW) body weights. Records were available for a total of 2075 lambs descended from 69 sires and 478 dams.

Animal management

Four hundred females were maintained in the flock during the period and reared under semi-intensive system of management. Males were selected based on 6MW, and their progeny performance was also considered for selection. Ten to 15 sires were kept for breeding per year and maintained 1:25 male to female ratio for breeding. Sires used for breeding were retained in the flock for at least 2 years; major and minor breeding seasons were March to May and July to September, respectively, during the study period. Twinning rate is very low in the flock. No selection criterion was applied for ewes. Females were bred either at an age of 15 months or after attaining 25 kg live weight. Ewes with poor growth and health were culled twice in a year. BW of newborn lamb was taken within 10 h of birth, and subsequent body weights were recorded, precisely when sheep attained 3, 6, 9 and 12 months of age.

Lambs were fed concentrate supplements ad libitum from 10 days after birth till weaning at an age of 3 months. After weaning, the lambs were fed with ad libitum green fodder, dry hays of horse gram and alfalfa and 300 g/day/head concentrate supplement. After attaining 6 months of age, sheep were kept under grazing for 8 to 10 h, but grazing time varied with season and ambient temperature. Grazing area consisted with deciduous vegetation and fodder tree like subabul (*Leucaena leucocephala*), neem (*Azadirachta indica*) and avisa (*Sesbania grandiflora*). Flock was supplemented with 300 g/head concentrate mixture in the evening hours. Apart from grazing, fodder tree loppings and hay of *Stylo hamata*, cow pea, horse gram and alfalfa were also fed to animals.

Statistical methods

Data were subjected to identify the fixed effects to be included in the model by least-square analysis of variance (SPSS 2005). Most decisive non-genetic factors affecting lamb's growth identified were year of birth, season of lambing, sex of lamb, dam's age, parity of dam and ewe's weight at lambing. Maternal components included in the models were fixed effects of year of lambing (eight levels), season of lambing (two levels), sex of the lamb (two levels) and parity of dam (seven levels). Ewe weight at lambing was kept as a covariate for BW and WW. Only significant effects ($p \leq 0.05$) were included in the models, and the same were subsequently used for genetic analysis (Table 1). Convergence of the restricted maximum likelihood (REML) solutions was assumed when the variance of function values (−2 log-L) in the simplex was less than 10^{-8}. To ensure that a global maximum was reached, the analysis was restarted. When estimates did not change up to two decimals, convergence was confirmed. Six models which accounted for the direct and maternal effects were fitted and are as follows:

$$y = Xb + Za + \varepsilon \qquad model\ 1$$
$$y = Xb + Z_a a + Z_m m + \varepsilon \text{ with } Cov(a_m, m_0) = 0 \qquad model\ 2$$
$$y = Xb + Z_a a + Z_m m + \varepsilon \text{ with } Cov(a_m, m_0) = A\,\sigma_{am} \qquad model\ 3$$
$$y = Xb + Z_a a + Z_{pe} pe + \varepsilon \qquad model\ 4$$
$$y = Xb + Z_a a + Z_m m + Z_{pe} pe + \varepsilon \text{ with } Cov(a_m, m_0) = 0 \qquad model\ 5$$
$$y = Xb + Z_a a + Z_m m + Z_{pe} pe + \varepsilon \text{ with } Cov(a_m, m_0) = A\sigma_{am} \qquad model\ 6$$

where, y was the vector of records, while b, a, m, pe and e were 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 Z_{pe}; A is the numerator relationship matrix between animals; and σ_{am} is the covariance between additive direct and maternal genetic effects. Assumptions for variance (V) and covariance (Cov) matrices involving random effects were as follows:

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

where, I represents identity matrix; $\sigma^2{}_a$, $\sigma^2{}_m$, Pe^2 and $\sigma^2{}_e$ are additive genetic variance, additive maternal, maternal permanent environmental and residual variances, respectively. The direct maternal correlation (r_{am}) was obtained for all the traits under analysis. Maternal across year repeatability for ewe performance was calculated for all the traits as t_m = (¼) $h^2 + m^2 + Pe^2 + r_{am}\ \sqrt{m^2}\sqrt{h^2}$ (Al-Shorepy 2001). The total heritability ($h^2{}_t$) was calculated using the formula: $h^2{}_t = (\sigma^2{}_a + 0.5\ \sigma^2{}_{am} + 1.5\ \sigma_{am})/\sigma p^2$ (Willham 1972).

The most appropriate model for each trait was selected based on likelihood ratio test of Meyer (1992). An effect was considered when its inclusion caused a significant increase in log-likelihood, compared with a model in which it was ignored. The significance of an effect was tested at $p \leq 0.05$ by comparing the differences in log-likelihoods (−2 log-L) with values for a chi-square distribution with degrees of freedom equal to the differences in the number of (co)variance components fitted for the two models. The model with fewest random terms was chosen where log-L values did not differ significantly. Estimates of (co)variance components were obtained by REML using WOMBAT software programme (Meyer 2007). Genetic parameters were estimated by fitting univariate and bivariate animal models including and ignoring maternal effects. Subsequently, a series of bivariate animal model analysis under the model 1 was carried out to estimate genetic and phenotypic correlations between the traits with starting values obtained from single trait analysis.

Results and discussion

All the fixed effects, viz. year of lambing, season of lambing, sex of lamb born and parity of dam, were significant for most of the growth traits of Nellore sheep (Table 2). Male lambs were heavier than females, and the differences were prominent with advancement of age, probably because of more variation in the endocrine system of both the sexes (Swenson and Reece 1993). Lambs born during major season had shown better growth performance than in other season. The dams with higher parity gave birth to heavier lambs than lambs of younger ewes. Year had significant effect on the growth pattern of lambs which indicates that the differences were due to late gestational nutrition of ewes and maternal body condition score prior to conception, seasonal grazing resources during late gestation and lambing and other environmental conditions during the period of study.

Estimations of covariance components and genetic parameters analyzed by univariate models for different growth traits of Nellore sheep are presented in Tables 2 and 3. Based on log-likelihood ratio test (LRT), the best model for BWT, 9WT and 12WT was model 2, whereas model 4 was appropriate for 3WT and 6WT and hence, the discussion of genetic parameters has been restricted to the best-fitted model only.

Pre-weaning weights

(Co)variance components and genetic parameters for BW derived from all six different models are presented in Table 2 with the best model based on LRT shown in bold face. The model including both direct additive genetic effects of lamb and maternal effects of the dam was sufficient to explain variation in BW of Nellore sheep. Direct heritability estimate obtained from model 2 for BW was found to be 0.08, and the corresponding maternal heritability estimate was 0.07; similar results were reported by Jafaroghli et al. (2010) in Moghani sheep. Lower estimates than those of the present study were observed in Kermani and Chokla sheep by earlier workers (Bahreini Behzadi et al. 2007; Kushwaha et al. 2009). On the contrary, higher than the present estimates was also reported in Malpura, Avikalin and Marwari sheep (Gowane et al. 2010b; Prince et al. 2010; Singh et al. 2016).

The incorporation of maternal genetic effects, maternal permanent environment effects and covariance of additive genetic and maternal effects increased the log-likelihood values and decreased the direct heritability values for BW considerably when compared with model 1. This observation confirms the proposal of Meyer (1992), who suggested that model 1 that did not account maternal effects resulted in overestimates of $\sigma^2{}_a$ and $h^2{}_a$. The inclusion of maternal genetic effects in model 1 inflated log-likelihood values substantially, and significant reduction of heritability estimates was observed compared to other models. This may be one of the reasons for lower heritability estimate obtained for BW in Nellore sheep in this study. The inclusion of maternal genetic effects in the model reduced the direct heritability values from 0.18 to 0.08. When models 4, 5 and 6 were applied for BW of Nellore sheep, noticeable changes were not observed in the log-likelihood values in

Table 1 Characteristics of the data structure and significance of the source of variation for growth traits in Nellore sheep

Traits[a]	BW	WW	6MW	9MW	YW
Number of records	2075	1945	1808	1647	1394
Sires with progeny records	69	69	68	68	67
Dams with progeny records	478	461	448	438	380
Animals with known paternal grand sire with progeny	1394	1320	1213	1135	997
Animals with known paternal grand dam with progeny	1328	1257	1152	1043	871
Animals with known maternal grand sire with progeny	1144	1068	975	917	776
Animals with known maternal grand dam with progeny	1026	938	851	772	613
Mean	3.1	13.27	18.04	22.68	25.92
Standard deviation	0.45	3.36	4.65	5.21	5.44
Coefficient of variation (%)	14.52	25.32	25.78	22.97	20.99
Effects[b]					
Year of lambing	**	**	**	**	**
Season of birth	**	**	NS	*	NS
Sex of lamb	**	**	**	**	**
Parity of dam	**	**	**	*	NS
Ewe weight (covariate)	**	**	**	**	**
Coefficient of determination R^2 (%)	46	50	51	53	55

NS non-significant ($P > 0.05$)

[*] $P < 0.05$

[**] $P < 0.01$

[a] BW birth weight, WW weaning weight (90 days), 6MW weight at 6 months, 9MW weight at 9 months, YW weight at 12 months

[b] Indicates the significance of the source of variation

comparison with model 2. In this study, larger environmental variation for BW was observed, and this might be due to the poor body condition score at conception and gestational nutrition of ewes (Gardner et al. 2007), and it suggests that less scope of genetic improvement would be expected in birth weight through direct selection.

The direct heritability estimate for WW observed in model 1 was 0.13. The addition of maternal genetic effect in model 1

Table 2 (Co)variance components and genetic parameters for pre-weaning growth traits of Nellore sheep

Trait	Model[a,b]	σ^2_a	σ^2_m	σ^2_{am}	σ^2_c	σ^2_e	σ^2_p	h^2	m^2	r_{am}	c^2	h^2_T	t_m	Log-L
Birth weight	Model 1	0.03				0.14	0.17	0.18				0.18	0.04	806.66
	Model 2	**0.01**	**0.01**			**0.11**	**0.13**	**0.08 (0.03)**	**0.07**			**0.11**	**0.09**	**1012.36**
	Model 3	0.01	0.01	0.00		0.11	0.13	0.10	0.10	−0.03		0.10	0.12	1012.76
	Model 4	0.01			0.01	0.11	0.13	0.10			0.07	0.10	0.10	1013.03
	Model 5	0.01	0.00		0.01	0.11	0.13	0.09	0.03		0.05	0.10	0.10	1013.36
	Model 6	0.01	0.03	−0.01	0.00	0.13	0.16	0.09	0.16	−0.39	0.02	0.10	0.16	823.93
WW	Model 1	1.01				6.68	7.69	0.13				0.13	0.04	−2950.58
	Model 2	0.01	0.70			6.00	6.71	0.00	0.10			0.05	0.10	−2829.70
	Model 3	0.10	0.80	−0.13		5.94	6.71	0.01	0.12	−0.02		0.05	0.02	−2829.45
	Model 4	**0.17**			**0.68**	**5.87**	**6.72**	**0.03 (0.02)**			**0.10**	**0.03**	**0.01**	**−2836.98**
	Model 5	0.01	0.65		0.08	5.97	6.71	0.00	0.10		0.01	0.05	0.11	−2829.65
	Model 6	0.02	0.76	−0.12	0.06	5.91	6.71	0.02	0.11	−0.45	0.01	0.03	0.11	−2829.42

[a] σ^2_a, $\sigma^2 m$, σ^2_c, σ^2_e and σ^2_p are direct 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 is σ^2_m/σ^2_p; t_m is maternal across year repeatability for ewe performance; h^2_t is total heritability and log-L is log-likelihood for the best model obtained from WOMBAT (Meyer 2007) and >WW is body weight of Nellore sheep at 3 months of age

[b] Column in bold values represents estimates from best model as per LRT. Values in the parentheses are standard errors

Table 3 (Co)variance components (kg^2) and genetic parameters for post-weaning growth traits of Nellore sheep

Trait[c]	Model[a,b]	σ^2_a	σ^2_m	σ^2_{am}	σ^2_c	σ^2_e	σ^2_p	h^2	m^2	r_{am}	c^2	h^2_T	t_m	log-L
6MW	Model 1	2.24				10.88	13.12	0.17				0.17		−3214.98
	Model 2	1.12	1.22			10.66	13.00	0.09	0.09			0.13	0.12	−3204.76
	Model 3	1.29	1.36	−0.21		10.56	13.00	0.10	0.10	−0.02		0.13	0.13	−3204.62
	Model 4	**1.59**			**0.86**	**10.57**	**13.02**	**0.12 (0.04)**			**0.07**	**0.12**	**0.10**	**−3211.98**
	Model 5	1.12	1.22		0.00	10.66	12.99	0.09	0.09		0.00	0.13	0.12	−3204.76
	Model 6	1.28	1.36	−0.21	0.00	10.56	13.00	0.10	0.05	0.30	0.00	0.13	0.09	−3204.62
9MW	Model 1	4.05				13.27	17.33	0.23				0.23	0.06	−3141.57
	Model 2	**2.77**	**1.33**			**13.09**	**17.20**	**0.16 (0.05)**	**0.08**			**0.20**	**0.12**	**−3136.33**
	Model 3	3.11	1.58	−0.35		12.88	17.22	0.18	0.09	0.00		0.20	0.14	−3136.21
	Model 4	3.33			1.07	12.80	17.20	0.19			0.06	0.19	0.13	−3138.70
	Model 5	2.28	1.22		0.11	13.05	17.19	0.16	0.07		0.01	0.17	0.12	−3136.31
	Model 6	3.11	1.50	−0.34	0.09	12.85	17.21	0.18	0.09	−0.16	0.01	0.19	0.12	−3136.20
YW	Model 1	3.52				13.42	16.94	0.21				0.21	0.05	−2649.08
	Model 2	**1.73**	**1.90**			**13.14**	**16.78**	**0.10 (0.05)**	**0.11**			**0.16**	**0.14**	**−2641.38**
	Model 3	1.66	1.74	0.20		13.20	16.79	0.10	0.10	0.01		0.17	0.13	−2641.33
	Model 4	2.26			1.71	12.76	16.73	0.13			0.10	0.13	0.14	−2643.76
	Model 5	1.76	1.59		0.40	13.01	16.76	0.11	0.10		0.02	0.15	0.15	−2641.25
	Model 6	1.68	1.44	0.19	0.39	13.06	16.77	0.10	0.09	0.12	0.02	0.16	0.15	−2641.20

[a,b] As indicated for Table 2

[c] 6MW, 9MW and YW are body weights at six, nine and 12 months of age, respectively, in Nellore sheep

did not increase the log-likelihood. Likewise, log-L value was not increased with all other models except with model 4, where inclusion of maternal permanent effect significantly and substantially increased the log-likelihood value. Direct additive heritability for WW derived from the best model (model 4) was 0.03 ± 0.02. Higher estimates than the present study were reported in Suffolk, Polypay, Chokla and Bharat Merino breeds of sheep (Notter 1998; Kushwaha et al. 2009; Gowane et al. 2010b), respectively. Lower estimates of h^2_a for WW than those of the present study were reported in Lori sheep by Mohammadi et al. (2015). Little genetic progress would be expected if selection is practiced for WW in this sheep. The estimate of h^2_m for WW (0.12) was in agreement with the results of Mohammadi et al. (2015). Higher values of maternal heritability than those of the present study were also reported (Bahreini Behzadi et al. 2007; Mohammadi et al. 2010; Li and Purvis 2012). A lower estimate of h^2_a for WW in our study was due to inclusion of maternal component in the model and also because of poor nutritional status of ewes due to poor pasture availability in grazing area, which generated larger environmental variations thereby obscured the actual genetic expression of lambs. Total heritability may be used to obtain breeding value and response to selection. The growth of Nellore lambs during pre-weaning period was completely relied upon dam's milk yield, and the maternal genetic effects were reduced markedly after weaning. This finding was in agreement with the reports of Mohammadi et al. (2010, 2013).

The Pe^2 estimate of 0.10 in the current study indicated that there is an inclining trend of maternal permanent effect on pre-WWs of Nellore sheep. Slightly lower estimates than those of our study were reported in Turkish Merino sheep (Ekiz et al. 2004; Ozcan et al. 2005), Bharat Merino (Gowane et al. 2010a) and Avikalin sheep (Prince et al. 2010).

For pre-WWs, r_{am} estimates were negative and moderate in magnitude especially for weaning weight (−0.45) which suggests that improvement in one effect will result in the decrement of another. Similar inference was drawn by Mandal et al. (2006b) in Muzaffarnagri sheep. Contradistinction between individual gene effects and maternal genetic component for a trait may be attributed to natural selection which usually favors an intermediate optimum (Tosh and Kemp 1994). Roff (2002) proposed that negative covariance among the traits could be due to linkage disequilibrium or antagonistic pleiotropy.

Repeatability of ewe performance (t_m) and total heritability h^2_t estimates for BW and WW were very low in magnitude leaving very little scope for further improvement of these traits. Gowane et al. (2010b) and Singh et al. (2016) reported higher estimates of t_m and h^2_t in Malpura and Marwari sheep, respectively.

Post-weaning weights

Estimations of (co)variance components and genetic parameters for the weights at 6, 9 and 12 months are shown in Table 3.

The heritability estimates for 6MW, 9MW and YW were 0.12, 0.20 and 0.16, respectively, and lesser than the estimates reported by Kushwaha et al. (2009), Prince et al. (2010), Mohammadi et al. (2015) and Singh et al. (2016) in Chokla, Avikalin, Lori and Marwari sheep, respectively, but higher than the estimate reported by Gowane et al. (2010a) in Bharat Merino sheep.

For 6MW, model 1 explains 17% of variance through direct heritability. The addition of Pe^2 to model 1 reduced the heritability from 0.17 to 0.12. Direct heritability from the best model was 0.12 ± 0.04. In this study, a Pe^2 estimate of 0.06 was observed, and permanent maternal effects were found to be diminished from 3 months to 6 months weight and negligible for weights at 9 and 12 months of age. Model 2 explains better regarding the variation affecting 9MW and YW. The inclusion of maternal genetic component to model 1 inflated log-likelihood values. With the advancement of age, direct heritabilities for body weights showed a tendency to increase because estimates of direct additive genetic variance component increased faster than the environmental variance components. This has been reported in several investigations (Mavrogenis et al. 1980; Yazdi et al. 1997; Bahreini Behzadi et al. 2007). In the present study, estimates of maternal heritability for all the traits were as large as the estimates of direct heritability, and a decreasing trend of maternal heritability estimates was observed from birth to 9 months of age. Lower estimates of maternal heritability for post-WWs were reported by earlier researchers for several sheep breeds (Snyman et al. 1995; Yazdi et al. 1997; Ligda et al. 2000; Neser et al. 2001; Ekiz et al. 2004; Bahreini Behzadi et al. 2007; Prince et al. 2010; Singh et al. 2016). Estimates of maternal heritability for yearling weights were high and unexpected because at these stage lambs are independent of their mothers and their performance should reflect only the direct effect of the genes on growth except for carry over maternal effects prior to weaning. Similar results, however, were reported by Snyman et al. (1995), Yazdi et al. (1997), Bahreini Behzadi et al. (2007) and Venkataramanan et al. (2015) for Afrino, Baluchi, Kermani and Sandyno sheep, respectively.

In the present study, higher estimates of maternal genetic effects than direct heritability estimates were obtained for all the growth traits. The maternal genetic effects were more evident during pre-weaning stage, and the same was reflected in the growth pattern of lambs at this stage. Maternal effects emanated during the pregnancy period, and lactation was receded at later stages, and its influence on lamb's declines as they grew older. These findings were in congruence with the proposition of Robison (1981) who confirmed that maternal effects in mammals were remarkable in growing lambs and dwindled at later stages but persisted even at older ages of considerable magnitude.

Estimates of repeatability of ewe performance were low in magnitude, and similar estimates were reported by earlier workers on different sheep breeds (Singh et al. 2016; Gowane et al. 2010b; Prince et al. 2010). Total heritability estimates for post-WWs were low to moderate in magnitude and were higher than the reports of Gowane et al. (2010a) for Bharat Merino sheep. However, Gowane et al. (2010b), Prince et al. (2010) and Singh et al. (2016) reported higher values in Malpura, Avikalin and Marwari breeds of sheep than those observed in Nellore sheep in the present study.

Correlation estimates

Genetic, phenotypic and environmental correlations for various weights at different ages of Nellore sheep were calculated by bivariate analysis under model 1 and are presented in Table 4. Genetic correlations of BW with WW (0.435), 6MW (0.622), 9MW (0.526) and YW (0.679) were high to moderate and suggested a strong genetic association without any antagonism among these traits. Hence, selection for any trait will bring improvement of another trait as all these traits were influenced by genetic factors in a similar order. The genetic, phenotypic and environmental correlations between the consecutive traits were higher than those of the non-consecutive traits. However, correlations of BW with other traits did not follow the above pattern (Boujenane et al. 2015; Li and Purvis 2012). The estimates of genetic correlation of WW with post-WWs such as 6MW (0.935), 9MW (0.845) and YW (0.79) were high and ranging from 0.84 to 0.90. The genetic correlation estimate of 0.41 between BW and WW was closer to the estimate of 0.56 by Hanford et al.

Table 4 Estimates of genetic (below the diagonal with residual correlations in parentheses) and phenotypic for different growth traits in Nellore sheep

Trait	Birth weight	WW	6MW	9MW	YW
Birth weight	–	0.36 ± 0.02	0.27 ± 0.02	0.236 ± 0.02	0.24 ± 0.02
WW	0.44 ± 0.17(0.35 ± 0.03)	–	0.76 ± 0.01	0.64 ± 0.01	0.59 ± 0.02
6MW	0.62 ± 0.14(0.19 ± 0.04)	0.94 ± 0.04(0.73 ± 0.02)	–	0.83 ± 0.008	0.64 ± 0.02
9MW	0.53 ± 0.14(0.17 ± 0.04)	0.85 ± 0.07(0.59 ± 0.03)	0.91 ± 0.03(0.81 ± 0.01)	–	0.86 ± 0.07
YW	0.68 ± 0.13(0.13 ± 0.04)	0.79 ± 0.08(0.52 ± 0.03)	0.85 ± 0.07(0.59 ± 0.03)	0.96 ± 0.02(0.83 ± 0.01)	–

For trait abbreviations, see footnote of Table 1

(2002) in Columbia sheep, 0.52 by Hanford et al. (2003) in Targhee sheep and 0.45 by Gowane et al. (2010a) in Bharat Merino sheep. The genetic correlations between other weight traits were positive and high in magnitude. The estimates observed in our study were in agreement with the findings of Gowane et al. (2010a) and Singh et al. (2016) in Bharat Merino and Marwari sheep, respectively. Moderate genetic correlation between WW and post-WW suggested that genetic factors influencing the body weight at weaning to adult age were same. The genetic correlations of BW and other traits were lower than the remaining traits, and it is also observed that genetic correlations of BW with other traits declined with increased age, which confirmed the research findings of Bahreini Behzadi et al. (2007) and Mohammadi et al. (2015). It implied that early expressed traits like birth weight and WW should be included in sheep recording system because of high genetic correlations among the traits in the present study. Shepherds in this region usually trade their sheep at an age of 6 months, and the additive genetic correlations between WW and 6MW and 9MW and YW traits were high in magnitude, which indicates that if selection is practiced at an age of 3 months, improvement would be seen at an age of 6 months.

Conclusion

The estimates of genetic parameters of Nellore sheep obtained in this study revealed that the maternal effects are having significant effects on body weights at birth and weaning ages. The maternal genetic heritability was found to be high in pre-WWs; hence, total heritability of the trait may be used in the selection of animals. Lamb weight at weaning was moderately heritable and had high positive correlation with later age groups and relatively low genetic correlation with birth weight. The estimates of heritability, phenotypic and genetic correlations among the different body weights indicated that the selection for improving the body weights at different traits should be done on the basis of 3-month weight because of higher heritability estimates and having higher genetic correlations with other traits.

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