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REGULAR ARTICLES

Direct and maternal variance components and genetic parameters for average daily body weight gain and Kleiber ratios in Nellore sheep

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Abstract
The objective of the present study was to estimate variance components and genetic parameters for average daily gain from birth to weaning (ADGa), birth to 6 months (ADGb) and 3 to 6 months (ADGc) and corresponding Kleiber ratios (Ka, Kb, and Kc) in Nellore sheep. Data were collected from the records maintained at Livestock Research Station, Palamaner, for analysis and the data spread from 1993 to 2016 (23 years). Lambing year, sex of lamb, season of lambing, and parity of dam were included in the model as fixed effects, and ewe weight was kept as a covariate. Six animal models were fitted with various combinations of direct and maternal genetic effects using restricted maximum likelihood procedure. The Akaike's information criterion was employed to determine the best model for each trait. Direct heritability estimates obtained in the study for ADGa, ADGb, ADGc, Ka, Kb, and Kc were 0.37, 0.41, 0.34, 0.48, 0.46, and 0.37, respectively, and their corresponding maternal heritabilities ranged from 0.11, 0.21, 0.11, 0.24, 0.22, and 0.11, respectively. (Co)variance among the direct and maternal effects were found to be negative in all the traits. Direct genetic correlations among the studied traits were positive with few exceptions, and they ranged from − 0.03 (Ka-Kc) to 0.99 (ADGa-Ka); similarly, the phenotypic correlations ranged from low to high − 0.18 (ADGa-Kc and Ka-Kc) to 0.95 (ADGa-Ka). These results indicated the importance of maternal effects in affecting the growth rate and efficiency of feed utilization traits and also suggested the possibility of moderate genetic progress for these traits through selection.

Keywords Average daily gain · Correlations · Heritability · Kleiber ratio · Nellore sheep · REML

Introduction

Nellore is tallest sheep breed in India, chiefly distributed in south coastal districts of Andhra Pradesh state, and its population was about 11.74 million heads and accounts for 19.17% of total sheep population of India (Livestock Census 2012). Animals of this breed are tall and white and black in color. They are primarily reared for mutton, well adapted to harsh environmental conditions of south coastal region of Andhra Pradesh state, and possess better disease resistance qualities. Major portion of income in sheep farming generated through trade of surplus male lambs. Hence, accelerated growth rate and better feed conversion efficiency are major components of a successful sheep enterprise. During the last few decades, shrinkage in the grazing area had resulted in tremendous rise in the cost of sheep enterprises. Hence, different strategies had emerged to improve the efficiency of meat production where the selection of animals is based on their growth rate and efficiency of feed utilization (Ghafouri-Kesbi 2011).

Kleiber ratio which is an indicator of feed conversion efficiency related traits can be expressed as a ratio of growth rate to metabolic weight (body mass$^{0.75}$) (Kleiber 1947), and it is widely being used in livestock breed improvement programs. Numerous studies revealed that Kleiber ratio is a moderately heritable and had strong correlation with growth traits. Hence, it is suggested to include in selection to bring progress in the feed efficiency without affecting growth rate and body weight (Abegaz 2005; Ghafouri-Kesbi et al. 2011).

Several investigations on growth and related traits of sheep stated that traits are markedly affected by both direct additive genetic effects and maternal genetic effects and models which ignored maternal genetic effects resulted in biased estimation of genetic parameters (Snyman et al. 1995; Yazdi et al. 1997;

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Abegaz et al. 2005; Prakash et al. 2012; Bahreini-Behzadi et al. 2014; Rashidi et al. 2008; Mandal et al. 2006; Kushwaha et al. 2009; Prince et al. 2010 and Singh et al. 2016). To formulate meaningful breeding plans, knowledge regarding (co)variance components and genetic parameters for economic traits related with growth rate is needed, and there was no objective information on genetic parameters for growth rate and feed conversion traits for this sheep breed. Hence, the current investigation was aimed to estimate the variance components and genetic parameters for average daily gain and Kleiber ratio in Nellore sheep by restricted maximum likelihood method by fitting six different models with exclusion and inclusion of animal and environmental effects, to estimate phenotypic, genetic, and environmental correlations among the traits and to identify the major non-genetic factors affecting these traits. The information obtained from this study will be useful for sheep breeders in implementing the optimum breeding strategies to bring genetic improvement of this sheep.

Materials and methods

Data collection

In this study, data were collected from the Nellore sheep flock maintained at the Livestock Research Station, Palamaner, Andhra Pradesh, India (located at13° 20′ E latitude and 78° 75′ N longitude at an altitude of 683 m above mean sea level). Different economic traits used for the analysis were average daily gain at various growth stages viz., average daily gain from birth to 3 months (ADGa), birth to 6 months (ADGb), and 3 to 6 months (ADGc) and their corresponding Kleiber ratios as Ka = $ADG_a/WW^{0.75}$, Kb = $ADGb/W6^{0.75}$, and Kc = $ADG_c/W6^{0.75}$. Data utilized for the study were spread over a period of 23 years from 1993 to 2016. Records were available for a total of 5033 lambs descended from 197 sires and 1515 dams.

Animal management

All the animals in the flock were reared under semi-intensive system of management. Four hundred breedable females were maintained in the flock over the years with male to female ratio for breeding was around 1:25. Ten to 15 sires were kept for breeding per year. Sires used for breeding were retained in the flock for at least 2 years, males were selected based on their 6 months weight, and their progeny performance was also considered for their selection. Breeding in the flock was confined to major (March to May) and minor seasons (July to September). Selection was not practiced for ewes. Females were bred either at an age of 15 months or after attaining 25 kg body weight. Culling was done twice in a year, and low production and poor health status were the basis for culling. Weight of new born lamb was taken within 10 h of birth, remaining weights at 3, 6, 9, and 12 months of age were recorded precisely on exact dates.

Weaning of lambs was done at an age of 3 months. Lambs were fed with concentrates (crude protein 18% and total digestible nutrients 70%) ad libitum from 10 days after birth till weaning. From 6 months of age, animals were sent for grazing on pastures consisting Stylo and Rhodes grass for a period of 8 to 10 h. During summer season, grazing was practiced during cooler hours of the day. In addition to this, 300 g of concentrate mixture was provided during post-weaning period. Fodder tree lopping and hay of *Stylo hamata*, cow pea, horse gram, and alfalfa were also fed to animals. Seasonal differences were observed in the growth patterns of animals during March to June due to limited grazing resources. Grazing area consisted with deciduous vegetation and fodder trees like Subabul (*Leucaena leucocephala*), Neem (*Azadirachta indica*), and Avisa (*Sesbania grandiflora*).

Statistical methods

Data were analyzed initially to identify the fixed effects to be included in the model by least-squares analysis of variance (SPSS 2010). The model included the 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. Only significant effects ($p \leq 0.05$) were included in the models which were subsequently used for genetic analysis. All fixed effects were significant for the considered traits with few exceptions. 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:

$$y = Xb + Za + e \quad (1)$$

$$y = Xb + Z_a a + Z_m m + e \ \text{with}\ Cov(a_{m,} m_o) = 0 \quad (2)$$

$$y = Xb + Z_a a + Z_m m + e \ \text{with}\ Cov(a_{m,} m_o) = A\sigma_{am} \quad (3)$$

$$y = Xb + Z_a a + Z_{pe} pe + e \quad (4)$$

$$y = Xb + Z_a a + Z_m m + Z_{pe} pe + e \ \text{with}\ Cov(a_{m,} m_o) = 0 \quad (5)$$

$$y = Xb + Z_a a + Z_m m + Z_{pe} pe + e \ \text{with}\ Cov(a_{m,} m_o) = A\sigma_{am} \quad (6)$$

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

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

where I represents identity matrix; σ^2_a, σ^2_m, σ^2_c, 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 $t_m = (¼)h^2 + m^2 + c^2 + r_{am}\sqrt{m^2}\sqrt{h^2}$ (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).

Estimates of (co)variance components were obtained by REML using wombat software program (Meyer 2007). Genetic parameters were estimated by fitting univariate animal models including and ignoring maternal effects. The Akaike's information criterion (AIC) was computed to rank the models. If p denotes the number of random (co)variance parameters to be estimated and log L is the maximized likelihood, then the information criterion is defined as: AIC = − 2 log L + 2p (Akaike 1974). The model yielding the smallest AIC explains better variation in the trait. Subsequently, a series of bivariate animal model analysis was carried out to estimate genetic and phenotypic correlations between the traits with starting values obtained from single trait analysis.

Results

The structure and number of records in pedigree, summary statistics, and significance of the source of variation for growth rate and Kleiber ratios obtained in the study in Nellore sheep are shown in Table 1. Number of animals in the pedigree was found to be 5033, and sires and dams with known progeny are 197 and 1515, respectively. The entire pedigree is distributed over 23 years, and the depth is fair and satisfactory which resulted in precise estimates of genetic parameters for the studied traits.

The least square means obtained in our study for ADGa, ADGb, and ADGc and Ka, Kb, and Kc were 113.31, 84.08, and 51.74 and 16.00, 9.43, and 5.70 g, respectively. Likewise, the coefficient of variation for the average daily gains and the Kleiber ratios were 33.75, 28.95, and 59.99 and 15.63, 11.45, and 54.04%, respectively. The coefficient of determination explains the efficiency of the model and the values for the traits ranged from 0.44 to 0.51% which explains the efficiency of the model.

Estimates of (co)variance components and genetic parameters resulted under different models are shown in Tables 2 and 3 along with log-likelihood values and AIC values. Generally, Eq. 1 which includes only animal additive genetic effects give biased results, whereas Eq. 2 consists both animal and maternal genetic effects may give better estimates of direct heritability. But in our study, we found that Eq. 3 resulted in lowest AIC values for all the traits and considered as the best model in explaining the variability in all the traits. This model includes animal and dam genetic effects along with the covariance between the effects. Equation 4 includes maternal permanent environment, Eq. 5 includes both dam genetic and environmental effects, and Eq. 6 includes all the effects along with the covariance between the effects. Equation 6 like Eq. 3 yielded better estimates, but based on the number of parameters utilized, AIC values, Eq. 3 is chosen as the best model.

Direct heritability estimates for ADGa, ADGb, and ADGc and Ka, Kb, and Kc obtained from the best model were 0.37, 0.41, and 0.34 and 0.48, 0.46, and 0.37, respectively, and the maternal heritability estimates for the above traits were 0.24, 0.22, and 0.11 and 0.11, 0.21, and 0.11, respectively. For all the studied traits, there was a strong negative correlation between and animal and maternal genetic effects and it ranged from − 0.99 to − 0.89. The total heritability is used in the computation of expected response to phenotypic selection for the traits and the estimates for the studied traits ranged from 0.10 to 0.15. Repeatability of ewe performance denotes the total maternal and ewe transmitted effects, and the estimates for the above traits were in the range of 0.00 to 0.06.

Estimates of correlations obtained from the bivariate analysis involving all the traits are presented in Table 4. Estimates of direct genetic correlations between the traits were almost positive, and the magnitude is very low to high; they ranged from − 0.25 (Ka-Kc) to 0.99 (ADGb-Kb), phenotypic correlations ranged from − 0.33 (ADGa-Kc) to 0.96 (ADGb-Kb), and likewise, the estimates of environmental correlations are from − 0.35 (Ka-Kc) to 0.95 (ADGa-Ka and ADGb-Kb).

Discussion

The overall least square means obtained in our study were in agreement with the findings of Prince et al. (2010), Savar-Sofla et al. (2011), Mohammadi et al. (2011), and Mandal et al. (2015). In the present study, estimates of coefficient of variation for average daily gains and Kleiber ratios from birth to 6-month period are low in magnitude and higher estimates obtained for post-weaning phase. Similar results were reported by Miraei-Ashtiani et al. (2007), Zamani and Mohammadi (2008), Savar-Sofla et al. (2011), Abbasi et al. (2012), and

Table 1 Characteristics of the data structure, summary of statistics, and significance of the source of variation for average daily body weight gain (growth rate) and Kleiber ratios in Nellore sheep

TRAIT	ADGa	ADGb	ADGc	Ka	Kb	Kc
Number of records	4349	3871	3871	4349	3871	3871
Number of animals in the pedigree	5033	4595	4595	5033	4595	4595
Sires with progeny records	197	194	194	197	194	194
Dams with progeny records	1515	1395	1395	1515	1395	1395
Animals with known paternal grand sire with progeny	2938	2552	2552	2938	2552	2552
Animals with known paternal grand dam with progeny	2683	2372	2372	2683	2372	2372
Animals with known maternal grand sire with progeny	2984	2557	2557	2984	2557	2557
Animals with known maternal grand dam with progeny	2826	2403	2403	2826	2403	2403
Mean	113.31	84.08	51.74	16.00	9.43	5.70
Standard deviation	38.24	24.34	31.04	2.50	1.08	3.08
CV (%)	33.75	28.95	59.99	15.63	11.45	54.04
Effects[a]						
Year of lambing	**	**	**	**	**	**
Season of birth	**	NS	**	**	NS	**
Sex of lamb	**	**	**	**	**	NS
Parity of dam	**	*	NS	**	*	NS
R^2 (%)	0.48	0.51	0.5	0.45	0.5	0.44

ADGa average daily gain from birth to weaning, *ADGb* average daily gain from birth to 6 months of age, *ADGc* average daily gain from 3 to 6 months of age, *Ka* Kleiber ratio associated to ADGa, *Kb* Kleiber ratio associated to ADGb, *Kc* Kleiber ratio associated to ADGc

***$P < 0.05$; $P < 0.01$; NS, non-significant ($P > 0.05$)

[a] Significance of the source of variation

Mandal et al. (2015). Growth rate and corresponding Kleiber ratios were higher in magnitude during the pre-weaning period of Nellore lambs than the post-weaning period. Similar results were reported by Ghafouri-Kesbi et al. (2011), Jalil-Sarghale et al. (2014), and Ghafouri-Kesbi and Gholizadeh (2017) in Iranian sheep breeds. Year of lambing had significant effect ($p < 0.01$) on all the studied traits; similarly, sex of lambs had significant effect ($p < 0.01$) on all the traits except for the Kleiber ratio for post-weaning period. With few exceptions, season of lambing and parity of dam are also found to be affecting the studied traits. The differences of growth rate during the different phases were due to the variation in environment and management conditions prevailed during those phases. In general, lambs suckled their mothers, and concentrate feed and chaffed green fodder were to be provided after 10 days of birth. During post-weaning phase, lambs were deprived of maternal support and had to depend upon themselves in procuring the feed and also they experience stress during grazing. Further the growth rate depended on availability of pasture and competition from grazing mates. Male lambs had shown better growth rates than females, and this is in agreement with the findings of Dass et al. (2004), Al-Bial et al. (2012), Ghafouri-Kesbi and Rafiei-Tari (2015), and Ghafouri-Kesbi and Gholizadeh (2017). The observed variation in different sexes can be attributed to the differences in their endocrine system. In females, estrogen hormone restricts the growth of long bones, whereas the testosterone had positive impact on growth rate and it acts like growth hormone in males (Fourie et al. 1970).

Parity of dam had significant effect on growth rate of lambs; similar finding was reported by Sezenler et al. (2016), and he opined that parity of ewe had significant effect on the daily milk yield of ewes during early lactation, and it is concluded that higher parity ewes produce more milk and provides required quantity of milk to their younger ones and may result in better growth rates. Year of lambing had significant influence on growth rate and the associated traits. The differences in the performances of lambs during different years suggested the differences in the different agroclimatic conditions, herd management, grazing pattern, nutrition, and breeding strategies. Similar findings were obtained by several authors (Dass et al. 2004; Al-Bial et al. 2012; Ghafouri-Kesbi and Gholizadeh 2017).

The direct heritability estimate obtained in the present study for ADGa was found to be 0.37. Literature suggested that the current estimate of direct heritability for ADGa were in the range of 0.03 in Sangsari sheep (Miraei-Ashtiani et al. 2007) to 0.46 in Moroccan-Timahdit sheep (El Fadili et al.

Table 2 Variance components and genetic parameters for average daily body weight gain (growth rate) traits of Nellore sheep

Trait	Model	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	AIC
ADGa	Model 1	1.26				7.01	8.27	0.15				0.15	0.04	− 5991.65	11,985.29
	Model 2	1.24	0.00			6.90	8.14	0.15	0.00			0.15	0.04	− 5971.01	11,946.02
	Model 3	*3.06*	*0.94*	*− 1.67*		*5.92*	*8.25*	*0.37*	*0.11*	*− 0.99*		*0.12*	*0.00*	*− 5937.61*	*11,881.22*
	Model 4	1.24			0.00	6.90	8.14	0.15			0.00	0.15	0.04	− 5971.01	11,946.02
	Model 5	1.24	0.00		0.00	6.90	8.14	0.15	0.00		0.02	0.15	0.06	− 5971.01	11,948.02
	Model 6	3.06	0.92	− 1.66	0.03	5.90	8.25	0.37	0.11	− 0.99	0.00	0.12	0.01	− 5937.6	11,883.20
ADGb	Model 1	83.76				378.22	461.99	0.18				0.18	0.05	− 13,744.9	27,491.89
	Model 2	84.73	19.35			360.85	464.93	0.18	0.04			0.20	0.09	− 13,737.2	27,478.38
	Model 3	*192.11*	*99.34*	*− 129.07*		*302.01*	*464.39*	*0.41*	*0.21*	*− 0.93*		*0.10*	*0.04*	*− 13,682.9*	*27,371.88*
	Model 4	82.25			7.81	372.02	462.08	0.18			0.02	0.18	0.06	− 13,744.4	27,492.83
	Model 5	84.82	19.30		0.00	360.82	464.95	0.18	0.00		0.04	0.20	0.09	− 13,737.2	27,480.38
	Model 6	192.24	99.38	− 129.15	0.00	301.93	464.41	0.41	0.21	− 0.93	0.00	0.10	0.04	− 13,682.9	27,373.88
ADGc	Model 1	113.64				698.32	811.95	0.14				0.14	0.04	− 14,853.8	29,709.55
	Model 2	113.64	0.00			698.32	811.95	0.14	0.00			0.14	0.04	− 14,853.8	29,711.55
	Model 3	*280.62*	*91.20*	*− 158.26*		*607.41*	*820.98*	*0.34*	*0.11*	*− 0.99*		*0.11*	*0.00*	*− 14,821.8*	*29,649.61*
	Model 4	113.64			0.00	698.32	811.95	0.14			0.00	0.14	0.04	− 14,853.8	29,711.55
	Model 5	113.64	0.00		0.00	698.31	811.95	0.14	0.00		0.00	0.14	0.04	− 14,853.8	29,713.55
	Model 6	280.63	91.20	− 158.26	0.00	607.41	820.98	0.34	0.11	− 0.99	0.00	0.11	0.00	− 14,821.8	29,651.61

Italic values represent estimates from best model based on AIC values

ADGa average daily gain from birth to weaning, *ADGb* average daily gain from birth to 6 months of age, *ADGc* average daily gain from three to 6 months of age

2000). Higher heritability estimate of ADGa suggested that growth rate during pre-weaning period was mostly affected by individual genes and maternal genes and less affected by environmental factors. Moderate heritability estimate for average daily weight gain of lambs during pre-weaning period in the present study suggested that better nutritional status and body condition scoring of ewe at lambing time had resulted in favorable environmental conditions which allowed the expression of animal own genes. Further, almost better environmental conditions in the flock increase the additive genetic variability and higher estimates of heritability would be obtained. Moderate heritability estimate for ADGa indicated that moderate genetic progress would be possible from selection. The permanent maternal environmental effects affecting ADGa accounted for only 6% of the total phenotypic variance in this study, and it is considerably small in magnitude when compared with the estimate of maternal heritability. Similar value was reported by Zamani and Mohammadi (2008) and Savar-Sofla et al. (2011) in other sheep breeds. Values higher than our estimate were reported by Ozcan et al. (2005) in Turkish Merino sheep (0.09), Mokhtari et al. (2012) in Arman sheep (0.12), Khorsand et al. (2014) in Afshari sheep (0.08), Mandal et al. (2015) in Muzaffarnagari sheep (0.10), and Mohsen and Farhad (2017) in Baluchi sheep.

Current heritability estimate for average daily weight gain (0.41) from birth to 6-month period in this sheep was in the range to that reported by Gizaw and Joshi (2004) in Menz (0.33) and Awasi×Menz (0.78) crossbred breeds of sheep. Lower estimates than our present findings were reported in Sangsari and Zandi sheep (Miraei-Ashtiani et al. 2007; Ghafouri-Kesbi 2011). The direct heritability estimate for post-weaning average daily body weight gain in the present study was 0.34. The results obtained were higher than those reported by Ghafouri-Kesbi (2011), Gizaw and Joshi (2004), Bosso et al. (2007), and Mohsen and Farhad (2017) in Zandi, Menz, Awasi×Menz, Djalonke, and Baluchi sheep breeds, respectively. Very low estimates were reported by Ekiz (2005) and Miraei-Ashtiani et al. (2007) in Turkish Merino (0.08) and Sangsari lambs (0.05), respectively. The lower estimates of heritability for post-weaning average daily body weight gain may be due to lack of favorable conditions during grazing, and also, the lambs were deprived of maternal support as the suckling of milk was stopped after weaning; further, animals weaned during summer may not gain body weight due to exposure to unfavorable conditions in the grazing field like scarcity of pasture and competition from grazing mates in the grazing area. During pre-weaning period, all the animals are reared almost under uniform favorable management conditions. Hence, the environmental differences among the animals were minimum leading to the better expression of animal genes, and thus, better heritability estimates could be obtained during this period. Whereas increased harsh environmental conditions in a population maximizes the residual variance and may yield lowered estimate of heritability during the

Table 3 Variance components (kg^2) and genetic parameters for Kleiber ratios of Nellore sheep

Trait	Model	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	AIC
Ka	Model 1	1.11				4.12	5.23	0.21				0.21	0.05	− 5705.68	11,413.36
	Model 2	1.47	0.47			3.89	5.83	0.25	0.08			0.29	0.14	− 5839.55	11,683.1
	Model 3	*2.54*	*1.25*	*− 1.59*		*3.08*	*5.29*	*0.48*	*0.24*	*− 0.89*		*0.15*	*0.06*	*− 5623.74*	*11,253.48*
	Model 4	1.07			0.24	3.93	5.24	0.20			0.05	0.20	0.10	− 5700.84	11,405.67
	Model 5	1.41	0.33		0.00	3.81	5.29	0.22	0.06		0.00	0.30	0.12	− 5684.39	11,374.78
	Model 6	2.54	1.17	− 1.56	0.10	3.04	5.28	0.48	0.22	− 0.91	0.02	0.15	0.06	− 5623.22	11,254.45
Kb	Model 1	0.19				0.78	0.97	0.20				0.20	0.05	− 1853.41	3708.82
	Model 2	0.20	0.04			0.75	0.98	0.20	0.04			0.22	0.09	− 1845.88	3695.756
	Model 3	*0.45*	*0.22*	*− 0.30*		*0.61*	*0.98*	*0.46*	*0.22*	*− 0.94*		*0.12*	*0.04*	*− 1787.88*	*3581.768*
	Model 4	0.19			0.02	0.77	0.97	0.19			0.02	0.19	0.07	− 1852.66	3709.324
	Model 5	0.20	0.04		0.00	0.75	0.98	0.20	0.04		0.00	0.22	0.09	− 1845.88	3697.756
	Model 6	0.45	0.22	− 0.29	0.00	0.61	0.98	0.46	0.22	− 0.95	0.00	0.12	0.04	− 1787.88	3583.758
Kc	Model 1	1.26				7.01	8.27	0.15				0.15	0.04	− 5991.65	11,985.29
	Model 2	1.24	0.00			6.90	8.14	0.15	0.00			0.15	0.04	− 5971.01	11,946.02
	Model 3	*3.06*	*0.94*	*− 1.67*		*5.92*	*8.25*	*0.37*	*0.11*	*− 0.99*		*0.12*	*0.00*	*− 5937.61*	*11,881.22*
	Model 4	1.24			0.00	6.90	8.14	0.15			0.00	0.15	0.04	− 5971.01	11,946.02
	Model 5	1.24	0.00		0.00	6.90	8.14	0.15	0.00		0.02	0.15	0.06	− 5971.01	11,948.02
	Model 6	3.06	0.92	− 1.66	0.03	5.90	8.25	0.37	0.11	− 0.99	0.00	0.12	0.01	− 5937.6	11,883.2

Italic values represent estimates from best model based on AIC values

Ka Kleiber ratio associated to ADGa, *Kb* Kleiber ratio associated to ADGb, *Kc* Kleiber ratio associated to ADGc

post-weaning period and in general, the additive genetic variability of a quantitative trait in a population changes with environmental differences, so the magnitude of heritability of metric traits also changes. Falconer and Mackay (1996) opined that environmental variance is a property of genotype up to some extent, where certain genotypes are more sensitive to the environmental differences, and it is concluded that post-weaning phase may generate huge variation in terms of environment and results in lowered estimates of heritability.

For pre-weaning Kleiber ratio, a higher estimate of direct heritability (0.48) was obtained in our study; similar estimate was reported by Talebi (2012) in Karakul sheep breed. Lower estimates (0.03–0.13) than the current study were also reported by Eskandarinasab et al. (2010), Savar-Sofla et al. (2011), Ghafouri-Kesbi (2013), Mohammadi et al. (2011), Mokhtari et al. (2012), Mohammadi et al. (2013), and Mandal et al. (2015) in various sheep breeds. Kleiber ratio from birth to 6-month period was observed to be 0.46. Lower estimates than our study were reported by Abegaz et al. (2005) in Horro sheep, Eskandarinasab et al. (2010) in Afshari sheep, and Mohsen and Farhad (2017) in Baluchi sheep as 0.01, 0.06, and 0.06, respectively. Our estimate of direct heritability for Kleiber ratio during post-weaning period was high in magnitude but lower than pre weaning phase. Very lower estimates than this study were reported by Ghafouri-Kesbi (2011)) and Mohsen and Farhad (2017) in Zandi and Baluchi sheep breeds, respectively. It is hypothesized that differences of efficiency of feed utilization among lambs are more conspicuous in post-weaning period than the pre-weaning phase, as the harsh environment and unfavorable conditions generates more differences.

The Kleiber ratio can be utilized in managing the feeding costs of sheep production enterprise as it enlightens how efficiently an animal converts the feed under low input ranging system (Mohammadi et al. 2011). Genetic improvement would be possible for the traits possessing better heritability and additive genetic variability as the Kleiber ratios in Nellore lambs are moderate to high in magnitude, they may be included in selection program to enhance the feed efficiency of the flock and a better selection response can be expected.

Maternal heritability estimate for all the growth rate and Kleiber ratio traits of Nellore sheep obtained in our study were almost similar to the findings reported by Ghafouri-Kesbi (2013) in Mehraban sheep. Usually, maternal effects emerge from the gene differences at different loci result in differences in the traits. It is suggested that the maternal genetic effects were reduced during post-weaning stage, and animals has to completely rely upon their own genes for better growth rate and improved feed efficiency. This finding was in agreement with the proposal of Mohammadi et al. (2010, 2013).

It is clearly understood that higher estimates were resulted from Eq. 3, indicating a very high negative covariance between direct and maternal effects. Hence, it is challenging to utilize both the effects to improve the traits in a selection program. Antagonism between the individual genetic effects and maternal effects of dam is the part of natural selection in

Table 4 Correlations between traits under yielded from bivariate analysis

Trait[a]		re	ra	rp
ADGa	ADGb	0.70 ± 0.01	0.78 ± 0.05	0.71 ± 0.01
ADGa	ADGc	− 0.11 ± 0.03	0.02 ± 0.14	− 0.08 ± 0.02
ADGa	Ka	0.95 ± 0.00	0.98 ± 0.00	0.96 ± 0.00
ADGa	Kb	0.66 ± 0.02	0.77 ± 0.05	0.68 ± 0.01
ADGa	Kc	− 0.35 ± 0.03	− 0.23 ± 0.13	− 0.33 ± 0.0.02
ADGb	ADGc	0.63 ± 0.02	0.64 ± 0.11	0.63 ± 0.01
ADGb	Ka	0.67 ± 0.01	0.76 ± 0.06	0.69 ± 0.01
ADGb	Kb	0.95 ± 0.00	0.99 ± 0.01	0.96 ± 0.00
ADGb	Kc	0.40 ± 0.02	0.41 ± 0.12	0.40 ± 0.02
ADGc	Ka	− 0.10 ± 0.03	0.007 ± 0.14	− 0.08 ± 0.02
ADGc	Kb	0.70 ± 0.02	0.73 ± 0.14	0.70 ± 0.01
ADGc	Kc	0.94 ± 0.00	0.96 ± 0.03	0.94 ± 0.00
Ka	Kb	0.70 ± 0.01	0.78 ± 0.07	0.71 ± 0.01
Ka	Kc	− 0.34 ± 0.03	− 0.25 ± 0.31	− 0.32 ± 0.02
Kb	Kc	0.42 ± 0.02	0.40 ± 0.12	0.41 ± 0.02

[a] For trait abbreviations, see footnotes of Tables 2 and 3

which the intermediate optimum will be mostly favored. Maternal permanent environment effects were low in magnitude during the pre-weaning phase, and it was zero during post-weaning phase, suggesting the importance of maternal environment at the time of birth and during lactation.

The total heritability is used in the computation of expected response to phenotypic selection for the traits. The estimates obtained in the study were moderate in nature and higher in magnitude than those reported by pre-weaning ADG (Mokhtari et al., 2012; Mohammadi et al. 2013) and Kleiber ratio (Mohammadi et al. 2010). The maternal across year repeatability (t_m) represents the total maternal effects, and ewe transmitted effects and lower estimates were obtained in our study than those reported by Ozcan et al. (2005), Safari et al. (2005), Mokhtari et al. (2012), and Mandal et al. (2015) in various sheep breeds.

With few exceptions, the genetic correlations between the traits were positive; few negative genetic correlations between the traits were observed in the study (ADGa-ADGc, ADGa-Kc, and Ka-Kc). High and positive genetic correlations were obtained for ADGa-Ka, ADGb-Kb, and ADGc-Kc, respectively. Similar results were reported by Ghafouri-Kesbi et al. (2011) and Abegaz et al. (2005) in Zandi and Horro sheep breeds, respectively. These results suggested that similar set of genes may be involved in controlling these traits. Phenotypic correlations were negative between pre- and post-weaning average daily gains, and phenotypic correlations between pre-weaning ADG and post-weaning Kleiber ratio were also negative and vice versa. These results were in conformity with the findings of Sinha and Singh (1997) in Muzaffarnagri sheep, Abegaz et al. (2005) in Horro sheep, and Mandal et al. (2015) in Muzaffarnagari sheep and Kleiber ratios. Abegaz et al. (2005) suggested that negative phenotypic correlations among the pre- and post-weaning ADGs would be resulted due to compensatory growth of some poorly nursed lambs in the post-weaning period in spite of positive genetic correlations, whereas both additive genetic and phenotypic correlations were negative for ADGa-Kc and Ka-Kc. This phenomenon could be explained by the phenomenon "pleiotropy" where the genes controlling these traits has positive effect on ADG and negative effect on Kleiber ratios and vice versa. Efficiency of feed utilization was higher during pre-weaning phase and was low during post-weaning period (Ghafouri-Kesbi et al. 2011). Further, it is recommended that selection should be done on average daily gain and the corresponding Kleiber ratio for birth to 6-month period instead of pre-weaning stage, as this period has positive genetic and phenotypic correlations.

The findings of the present study suggested that the environmental factors also had a role on growth rate and Kleiber ratios in Nellore lambs. Both direct and maternal genetic effects were found to be important in the analysis of growth rate traits and Kleiber ratios. Moderate genetic variability and heritability were observed in all the studied traits. Hence, moderate genetic improvement in these traits would be possible by selection. The sheep production system is in a transition phase in India, where the management systems of sheep tend to shift towards intensive system from migratory and semi-intensive system where the expenditure of sheep production will be on higher side. Hence, Kleiber ratio which is an indicator of efficiency of feed conversion could be utilized in the selection program to bring improvement in the biological efficiency of the flock. Negative correlations between the pre- and post-weaning growth traits should be considered while implementing the breeding strategies. Average daily gain and Kleiber ratios from birth to 6-month period should be considered as heritability estimates, and also, positive genetic and phenotypic correlations were moderate in nature.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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